VOCAL RESPONSE TIMES TO ACOUSTIC STIMULI IN WHITE WHALES AND BOTTLENOSE DOLPHINS

A Dissertation

by

DIANE JOYNER BLACKWOOD

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2003

Major Subject: Wildlife and Fisheries Sciences

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Approved as to style and content by:

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ABSTRACT

Vocal Response Times to Acoustic Stimuli
in White Whales and Bottlenose Dolphins. (December 2003)
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Response times have been used to explore cognitive and perceptual processes since 1850 (Donders, 1868). The technique has primarily been applied to humans, birds, and terrestrial mammals. Results from two studies are presented here that examine response times in bottlenose dolphins (*Tursiops truncatus*) and white whales (*Delphinapterus leucas*). One study concerned response times to stimuli well above the threshold of perceptibility of a stimulus, and the other concerned response times to stimuli near threshold.

Two white whales (*Delphinapterus leucas*) and five Atlantic bottlenose dolphins (*Tursiops truncatus*) were presented stimuli well above threshold. The stimuli varied in type (tone versus pulse), amplitude, duration, and frequency. The average response time for bottlenose dolphins was 231.9 ms. The average response time for white whales was 584.1 ms. There was considerable variation between subjects within a species, but the difference between species was also found to be significant. In general, response times decreased with increasing stimulus amplitude. The effect of duration and frequency on response time was unclear.

Two white whales (*Delphinapterus leucas*) and four Atlantic bottlenose dolphins (*Tursiops truncatus*) were given audiometric tests to determine masked hearing thresholds in open waters of San Diego Bay (Ridgway *et al.*, 1997). Animals were tested at six frequencies over a range from 400 Hz to 30 kHz using pure tones. Hearing thresholds varied from 87.5 dB to 125.5 dB depending on the frequency, masking noise intensity and individual animal. At threshold, median response time across frequencies within each animal varied by about 150 ms. The two white whales responded significantly slower ($\sim$670 msec, $p<0.0001$) than the four dolphins ($\sim$410 msec). As in terrestrial animals, reaction time became shorter as stimulus amplitude increased (Wells, 1913; Stebbins, 1966).

Across the two studies, the dolphins as a group were faster in the above-threshold study than in the near-threshold study. White whales had longer response times than bottlenose dolphins in both studies. Analysis of response time with an allometric relation based on weight shows that the difference in weight can explain a significant part of the difference in response time.

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Wesley R. Elsberry wrote the BREAC application used for the hearing test data collection, generated several of the illustrations used here, and provided general support.

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CHAPTER I

INTRODUCTION

Understanding how animals process information can help in understanding how animals perceive loudness at different frequencies in different background noise. One conceptual tool in research has been the time an animal takes from being presented with a stimulus to emitting a response, or *response time*.

A. Review of response time literature

The idea of using reflex in analyzing information processing goes back to at least Galen (Posner, 1978). Until the mid 1800s, researchers thought that nervous processes were immeasurably fast. In the early 1840s, Johannes Müller thought that the time for nerve conduction was similar to the speed of light and therefore could not be measured. Müller's student, Hermann Ludwig Ferdinand von Helmholtz, measured time for conduction in frogs and humans at about 100 m/s in 1850 (Donders, 1868).

The pursuit of astronomy raised the issue of response times in humans. In 1795, Nicholas Maskelyne and his assistant disagreed about the transit time of a star (the time at which a star apparently crossed the meridian) (Wells, 1913). F. W. Bessel, an astronomer at Könisberg, began a study of response times in 1820 due to his interests in the accuracy with which he and his colleagues recorded the times of stellar transits. Astronomers at that time listened to the ticking of a metronome to estimate the exact time at which a star passed the hairline of their telescope. They judged the point of time between one second and the next as best they could. When Bessel compared his times to that of a visiting astronomer, large discrepancies were obvious, with Bessel always judging the transit earlier. The findings intrigued Bessel and he termed the

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This dissertation follows the style of the Journal of the Acoustical Society of America.

difference in response time the "personal equation" (Brebner and Welford, 1980).

B. General methods in past response time studies

Brebner and Welford (1980) defined response time as the time from onset of a stimulus or signal to initiation of response. Response time has been recognized as a way to relate mental events to physical measures since the mid-nineteenth century. Researchers have wondered why response time is longer in some situations than in others, and what is being done with the additional time. A variety of methodological approaches have been used over the history of research on response times.

Subject response behaviors have varied across studies of response time. Netsell and Billie (1974) reviewed several studies in presenting results of their work on response times for a speech task in humans. Netsell and Billie (1974) found the mean response time for a speech task was essentially the same as finger movement response times reported in experimentally similar studies (Botwinick and Thompson, 1966; Luschei *et al.*, 1967). Siegenthaler and Hochberg found the response time to push a plunger 1 mm with tongue tip was 130 ms (Netsell and Billie, 1974). Shervanian and van den Berg studied response times of speech muscles and found that respiratory muscles had the fastest response times (123 ms) and lip closure the slowest (170 ms) (Netsell and Billie, 1974). Ladefoged (1960) measured the time between intercostal EMG onset and voice onset in a response time task with a auditory stimulus. The time to EMG onset varied from 140 to 320 ms, while the mechanical response time (EMG onset to voice onset) "was comparatively constant at 48 ms". A nose key was employed by Young (1980) in a study of response times in chinchilla. Response time studies in pigeons typically use a key peck (Blough, 1992).

Different methods of stimulus presentation have been employed in response time

studies. Typically, discrete trials are used in which a cue in a different sensory modality than the stimulus is given, then the stimulus, and the subject's response is noted. In most non-human studies, a reward for each correct responses is given.

In human studies and uncommonly in animal work, a method of *free response* is utilized. Egan *et al.* (1961) defined the method of free response, with several distinguishing characteristics. A weak signal is presented several times with a random temporal pattern with a background of noise within a long (>= 2 minutes) observational period. The listener does not know when a tone will occur or how many tones will be presented. The listener emits a single response upon hearing a tone. This listening situation is more difficult to analyze because a trial is not defined. A procedure is needed to separate responses between hits and false alarms. The method of free response is similar to situations in every day perception. Clinical hearing studies often use a method of free response.

In simple response time (SRT) studies, it is typical that there is high variability and often a skewed distribution in response times even in the same subject. A number of different analytical methods have been proposed to deal with this variability. Many of these utilize some sort of measure of central tendency, and then statistics are performed on the summary data. Measures which have been proposed and used in the literature include the mean (Ridgway *et al.*, 2001), the median (Birren and Botwinick, 1955; Costa *et al.*, 1964; Stebbins and Reynolds, 1964; Weiss, 1965), quartile or stanine level (Young, 1980), geometric mean (Humes and Ahlstrom, 1984), and means of log-transformed data (Gosling and Jenness, 1974).

Outliers are response times generated by processes other than the ones being studied. Outliers can be produced by subject inattention, guesses on detection, anticipation, or guesses on failure to reach a decision. Removal of outliers is desirable for most empirical or theoretical purposes. Ratcliff (1993) explored the effects of

various methods of removing outliers for data sets that did and did not contain extraneous data (actual outliers). The article deals with the purely practical question of improving the power of analysis of variance, the effects of outliers on descriptive statistics, and the issue of fitting explicit models to distributions that may contain outliers. Long spurious outliers can be difficult to separate from valid long responses. Most response time studies include some form of upper cutoff for length of response time. Cutoffs based on standard deviations and transformations were also examined. No single method had the best results for the various data sets tested. The median is least influenced by outliers and cutoffs.

C. Biological meaning of the different response times

Response time has long been used to measure neural processing, beginning with von Helmholtz's measurement of nerve conduction speed. The perceptual and cognitive processes that intervene between stimulus and response must take some time. Adding, deleting or altering one of these processes should affect response time (Donders, 1868). While *response time* (RT, also known as *reaction time*) has been a popular dependent variable in studies of human perception and cognition, only limited work had been done on non-humans (Blough and Blough, 1978). Choice and rate measures are more commonly used in non-human studies. Choice provides binary data (go/no-go, left/right, yes/no, etc). Continuous values can be extracted by averaging over many trials, but the information from a single trial is limited. *Response rate* provides a continuous measure and can be very informative, but requires integration over many trials.

Response time contains information from a continuously variable quantity in one response. Response time must reflect the duration of some combination of the processes needed to generate the response. However, the nature of those processes and their combination may still be unclear.

D. Response time components

Helmholtz invented the *subtraction method* of response time analysis in 1850 (Swanson *et al.*, 1978) to attempt to measure nerve conduction. In the subtraction method, response times for a cognitive task are measured as well as response times for separate components of the complex task. Estimates of time required for cognitive processing of component tasks is found by subtraction.

Researchers have proposed decomposition of response time into component parts. *Sensory time* (from stimulus onset to evoked sensory potential from the cortex) ranges from 30 to 40 ms (Miller and Glickstein, 1966). *Organizational time* is the time between the onset of the evoked sensory potential and the onset of the motor potential from scalp electrodes (Vaughan *et al.*, 1965) or pyramidal tract neuron discharges (Evarts, 1966; Humphrey *et al.*, 1970; Luschei *et al.*, 1971). *Motor time* (time from motor cortex cell discharge to onset of electromyographic (EMG) activity at the muscle of interest) was estimated at 30 to 50 ms (Netsell and Billie, 1974). Organizational response time can also be estimated by *subtracting* motor and sensory time from total response time.

The subtractive method was extended to the cognitive domain in 1868 by Donders in attempt to separate stimulus detection, stimulus discrimination, and response selection. In 1912, Poffenberger used subtraction in an attempt to measure the time taken to traverse a synapse in the corpus callosum (Poffenberger, 1912). The first

trials were non-shock trials. The median time from these trials was used to set the shock criteria in shock trials. The subject received a mild shock if they failed to respond soon enough. Weiss (1965) divided response time into motor and pre-motor time. Motor time was from the onset of EMG activity of the extensor digitorum communis of the preferred hand to when the subject released the key. Pre-motor time was the time from the onset of the stimulus to the onset of EMG activity. Motor time varied little between shock-motivation and non-shock conditions. Motor time showed no significant difference over four preparatory intervals of 1, 2, 3 and 4 seconds. The pre-motor time was significantly slower ($p<0.001$, $F=12.81$, $df=3$) for shorter preparatory intervals. Motor time did not differ significantly between shock-motivation and non-shock conditions. Non-shock pre-motor times were significantly slower ($p<0.001$) than shock-motivated response times, 109.3 and 97.7 ms respectively for the younger age group.

E. Information theory and response time

Psychologists began to resurrect the use of response time in relation to the new mathematical theory of information. Claude E. Shannon proposed a formal and quantifiable measure of *information* in 1948 (Shannon, 1948). Working from a set of assumptions of the desired properties of a measure of information, Shannon defined an equation which yields the *entropy* of a message or sentence composed of a series of symbols. This quantity, designated by the letter H, is in units of bits per symbol in the message. A *bit* or *binary digit* is the standard unit of information, comprising the amount of information that can be represented by the state of an on/off device, like a switch.

$$H = -k \sum_{i=1}^{n} p_i log_2 p_i \tag{1.1}$$

where k is a positive proportionality constant and p_i is the probability of the ith symbol.

The properties of H are that it is at a minimum for messages with no uncertainty (that is, when a message consists entirely of repeats of one symbol), and at a maximum when there are multiple symbols in a message and they all occur with equal likelihood (Shannon, 1948).

Shannon information is not the only formal account of information. Kolmogorov, Solomonoff, and Chaitin each independently developed another account based upon a quantifiable length of a description of a message. Termed *algorithmic information theory* (AIT), this approach is based upon finding the minimum length Turing machine program that will emit the message (Gammerman and Vovk, 1999). The primary difference between these concepts is that Shannon information is firmly based on a probabilistic approach and AIT is thoroughly non-probabilistic.

The idea that response time was linearly related to amount of information transmission was suggested by Hick and Hyman in the early 1950s. In 1885 Merkel (as reported in Hick (1953) and Hyman (1953)) studied choice response time in humans, looking at 1 to 10 alternatives. His data demonstrated that when a subject responds to one stimulus from a number of equally probable alternatives, the response time increases with the number of alternative stimuli and corresponding responses.

(Hick, 1953) investigated response times and gain of information in terms of Shannon information. An event whose probability is p has a corresponding amount of information of -log(p). This definition is independent of the physical and psychological world to keep the definition general about information rather than restricting it to

a type of information. The probability makes it a measure of prior expectation, and thus the information learned is zero when an event is certain to happen, and high when it is unlikely to happen.

Hyman (1953) proposed that choice response time experiments can be looked at as a model of a communication system. Each alternative stimulus represents a message. The mean information accompanying the presentation of a single stimulus was varied by (1) varying the number of equally probable alternatives; (2) altering the probability of occurrence of particular stimulus/choices; and (3) including sequential dependencies between successive choices and alternatives. Hyman proposed that response time is a direct function of the amount of information in the stimulus series; and the regression of response time to amount of information per stimulus is the same no matter which of the three methods is used to manipulate the information in the stimulus. This study required errorless performance by the subjects. Subjects were given practice on similar data sets of light stimuli, but they were never given the same series twice and were instructed on the statistical probability of the series. The subject responded by saying the name of the light stimulus into a microphone. In experiment one, the number of equally probably stimuli varied from one to eight. The respective bits of information were 0.00, 1.00, 1.58, 2.00, 2.32, 2.58, 2.81 and 3.00. In experiment two, both the number of alternatives and the probabilities changed such that the respective bits of information for the eight conditions were 0.47, 0.72, 0.99, 1.39, 1.75, 2.16, 2.38 and 2.75. In experiment three, there were different numbers of alternatives that all occurred equally often. But, the probability of occurrence of a particular stimulus depended on the immediately preceding stimulus. The respective bits of information in experiment three were 0.72, 0.92, 1.36, 1.79, 2.21, 1.00, 2.00 and 2.81.

Linear correlation between response time and bits of information by subject and experiment resulted in r^2 values between 0.874 and 0.991. In experiment three, several conditions included "no immediate repetition". In terms of information theory, this lowers the amount of information more than if the same stimulus could repeat. However, this restriction increased the response time. The three regression lines (from the three experiments) were found to coincide for three subjects.

Hick and Hyman both directed their attention to choice response times, but they also considered the case of simple response times. Simple response times pose a problem in terms of Shannon information. Within a choice response time task, n is the cardinality of set of discrete stimuli presented with corresponding trained responses. the number of types of stimuli, n, is 1, $\log(n)$ is zero, which predicts a zero response time for simple response time. But this does not take into account all of the display energy, and the possibility of "no stimulus" at any time when waiting for a stimulus. If the possibility of "no stimulus" is assumed to have equal probability to that of each of the possible stimuli, then a Shannon measure of information can also be applied to simple response time data. Hick assumed that $n+1$ could usefully describe simple response times, in that the uncertainty of when a stimulus would be presented could be taken as equivalent to a second stimulus in its effect on response time. Hick found that a good fit to a body of data collected by Merkel could be had by the following equation:

$$RT(seconds) = 0.626\ log_{10}(n+1) \tag{1.2}$$

Hick also tested an equation, A + B log(n) which was put forth by V. R. Cane and found it gave a slightly worse fit. Hick indicated that it could still be considered as an explanation of the data. Hick's stimuli were controlled by paper tape and given

at equal intervals. When there was only one response choice (simple response time) the paper tape was actually for two choices, so the time of the stimulus for response would be variable.

Simple response time for Hick's data was 156 ms with fingers on switches. Simple response time for Merkel's data was 188 ms. The simple response time for Hyman's data was about 220 ms.

Rees (1971) looked at choice response time in spastic hemiplegics. As the number of choices (1, 2, 4 and 6) increased, the total response time, recognition time and movement time all increased for both affected and non-affected hands. There was a good fit for linear regression on the relationship between information (0 to 2.58 bits) and response time (277 to 388 ms).

Vickrey and Neuringer (2000) examined Hick's law in pigeons and found response times increased as a linear function of $\log_2$(number of potential target stimuli) as predicted by Hick's law. The values of slopes and intercepts decreased with training. Differential reinforcements for response times under a percentile reinforcement contingency also decreased the slopes and intercepts.

Typical experimental design for choice response times involves multiple different stimuli and an equal number of different responses to be made by the subject. Typical experimental designs for simple response time vary a property of a single stimulus type, and the subject has a single response type to be made. The experimental design of the studies described here do not conform completely to either of these. Acoustic stimuli of different frequencies correspond to part of the choice response time paradigm, but the subjects have only a single response to be given on perception of any of the different stimuli. The use by Hick of Shannon information should be applicable, since his relation only refers to number of stimuli rather than to number of possible responses.

F. Factors affecting response time

Response times may be affected by a variety of conditions. The subject's internal state (age, degree of accommodation to conditions, drugs, hormones, fatigue, vigilance, etc.), the properties of the stimuli (amplitude, duration, frequency, color, etc.), and properties of the environment may all contribute to differences in response times.

1. Internal state

Studies have compared response times of humans in different age groups.

Bellis (1931) studied the relationship between chronological age and response time in 150 humans aged 4 to 60 years in a visual and auditory simple response time task. The individual's time was the mean of the fastest 5 responses. Response time for males was faster than females in early childhood and late maturity. Response time to sound was faster than to light. The fastest group, males 21 to 30 years, responded to sound in 190 ms and light in 220 ms. The slowest group, females 4 to 10 years (mean age 5.4 years), responded to sound in 590 ms and light in 620 ms.

Birren and Botwinick (1955) studied the effect of age on finger, jaw and foot response time. The preparatory interval was from 1 to 6 seconds. A 1 kHz 200 ms tone was delivered to the human subject via ear phones. Each white male human subject made 150 responses, 25 each in order for finger, foot, jaw, foot, jaw and finger. There were two groups, 32 aged 18 to 36 years and 32 aged 61 to 91 years. The older subjects (182 ms finger, 194 ms jaw, and 202 ms foot) were significantly slower than the younger subjects (232 ms finger, 254 ms jaw, and 260 ms foot)in all three response times. There was no significant difference between younger and older subjects caused by increased path length of the peripheral nervous system. Birren concluded his results indicated that the slowing of response time with age is primarily

in the central nervous system.

Weiss (1965) also found that response time got longer with age in humans in a finger lift response time task. Weiss compared two groups of male humans aged 18 to 30 years and aged 65 to 80 years. The median after the first data set after a practice series was used to set a time when the subject received mild shock if they failed to respond. The response time without shock for the older group (227.8 ms) was significantly slower ($p<0.001$) than for the younger group (173.9 ms). The response time with shock-motivation for the older group (196.2 ms) was significantly slower ($p<0.001$) than for the younger group (156.5 ms). Times reported are the means across subjects of the medians within subjects.

Degree of light adaptation has been shown to affect response times to visual stimuli. A *threshold* is a value of a property of a stimulus such that 50% of stimuli at that value are perceived by the subject. Braun *et al.* (1996) found that light adapted subjects responded faster to dim targets (near detection threshold) in the right visual field and that dark-adapted subjects responded faster to dim targets (equally near detection threshold) in the left visual field. A possible explanation could be rod-mediated versus cone-mediated response time and the differences in rod/cone concentrations in various parts of the visual field.

The presence of certain drugs affects response times with alcohol being one of the drugs most frequently studied. The effect of alcohol has been examined in humans and rats. Gustafson (1986) compared two alcohol levels (0.33 and 1.00 ml/kg body mass or 0.022 and 0.088 percent blood alcohol respectively) to the same human subject with a placebo in a vigilance setting. During the first 5 minutes of the task, the mean response time was about 202 ms for the control and the 0.33 ml/kg and the control group and about 207 ms for the 1.0 ml/kg group. Response time increased pronouncedly with time on task (5 minute intervals for total of 30 minutes) for the

1.0 ml/kg group. There was a small and insignificant increase over time for the other two groups. After 25 minutes, the 1.0 ml/kg group response time was about 253 ms while the other two groups were still about 210 ms. The alcohol appeared to have a greater effect on tasks lasting longer than 10 minutes. Stebbins *et al.* (1960) examined response time in rats to visual stimuli. He found that the response time (1.8 s) of rats was slower when injected with 3 ml of 20 percent ethyl alcohol intraperitoneally than response time (1.4 s) when injected with 3 ml of saline. The long term or vigilance effect of alcohol on rats was not examined.

2. Properties of stimuli

In early response times studies, it was difficult to precisely control properties of stimuli. The difficulty of calibrating stimulus properties may introduce unwanted artifacts in experimental procedures. For tonal acoustic stimuli, the parameters that are usually under experimental control are amplitude, duration, and frequency.

The earliest person to experiment on the effects of duration on response time was Sven Froeberg. He looked at duration in visual stimuli with durations of 48, 24, 12, 6, and 3 ms with a constant intensity, 3 mm square stimuli. Froeberg (as reported in Wells (1913)) concluded that response time increased by approximately equal increments as the duration of the stimulus decreased geometrically. This held over a limited range. The increase in response time became more rapid as threshold was approached.

Wells (1913) was interested in the difference in response time to light and sound. Some people speculated that response time was faster to light because the effect of the stimulus on the retina was probably of longer duration than the effect of sound on the hearing mechanism. Little attention had been paid to duration with some speculating that increasing duration would have the same effect as increasing

amplitude. By 1913, it had already been established that response time was inversely related to stimulus amplitude. Wells examined durations from 10 ms to 150 ms and 1000 ms with response times ranging from about 106 ms to 210 ms (not respectively). Wells's data does *not* support a rule analogous to Weber's law which Froeberg's data followed. There is no evidence of increase in response time with decrease in duration. There is some trend to support that the longer the duration, the longer the response time. In auditory response times to varying duration, Wells found no pattern.

Mean response times of 20 trials for 72 human subjects to fixed duration stimuli of 100, 200, 400, 800, 1600, and 2400 ms was 192.5, 196.7, 196.0, 206.3 and 209.2 ms respectively (Gregg and Brogden, 1950). This result indicates that response time to a fixed duration stimulus increases linearly as the duration increases geometrically.

Wells (1913) reviews support for the idea that response time varies inversely with visual stimulus intensity, more markedly as threshold is approached. Wundt found that response time decreased as weak electrical stimuli increased in intensity. With further increase in electrical stimuli, response time will increase. Exner believed that a very strong stimulus which produced a shock produced a great shortening of response time. Martius concluded that practice and attention will equalize response times to different intensities of tones within a scale used (as reported in Wells (1913)). Slattery measured response time to different intensities of tones, tones of different pitch, and electrical stimuli of different intensities and concluded that response time does not vary with intensity to any degree that can be detected. Slattery had only a few subjects.

Froeberg studied variations in intensity and duration of visual and auditory stimuli (Wells, 1913). He also examined the effect of the size of visual stimuli. The time of response increased arithmetically with geometrically decreasing size of the 5 sizes of stimuli studied. Textbooks in 1913 usually take for granted that as a

general rule, response time varies inversely with the intensity of the stimulus. Wells (1913) provided three supporting examples: *Principles of Psychology* (James, 1890, Vol. 3, p.96); Külpe's *Outlines of Psychology* (Külpe, 1895, p. 407); and *Elements of Physiological Psychology* (Ladd and Woodworth, 1911, p. 479).

Cattell (1886b,c) studied response time to various intensities of light, sound and electrical stimulation on humans. He generally found a faster response to higher amplitude stimuli. His response times were on the order of 150 to 200 ms, however, his stimuli were not calibrated.

Cattell (1886b,c) did not find a difference in response time to different colors of light. Homes (1926) concluded that human response time to various colors was not a function of the wave-length of light when balanced for intensity.

In many simple response times studies, subjects are given a warning signal to let them know that test stimulus will appear shortly. The time between the warning signal and the test stimulus is called a preliminary interval or a foreperiod. Usually the warning signal is in a different sensory modality than the test stimulus. For instance, when studying simple auditory response time the warning signal is often a light.

Minimal response times appear after a foreperiod in the middle of the possible range of foreperiods or response times continue to decrease as foreperiods increase, depending on the specific range and experimental design (Hohle, 1965). The prior-preliminary interval (from the previous trial) also may influence response time. Response time was reduced when prior-preliminary interval was short relative to the current preliminary interval.

Gosling and Jenness (1974) studied the effects of preliminary interval (PI) and prior-preliminary interval (PPI). Preliminary intervals were 0.5, 1.5, 3.5, 5.5, 8.5 and 10.5 sec. Response time decreased significantly ($p<0.001$) from 256 to 247 ms as

preliminary interval increased from 0.5 to 10.5 sec for normal human subjects. The mean response time increased significantly ($p<0.001$) from 250 ms to 262 ms as prior-preliminary interval increased from 0.5 to 10.5 sec. Fastest response times occurred when short prior-preliminary intervals preceded long preliminary intervals.

Cattell (1886b,c) also found choice response time was typically slower than simple response time. He noted difficulty in obtaining accurate measurements of characteristics of the stimuli and of the response time with available equipment.

G. Applications of response time studies

Response time information has been used to measure nerve conduction, to measure hearing in non-verbal children, investigate the effect of brain lesions, and to test hearing devices.

1. Nerve conduction

Helmholtz invented the subtraction method of response time analysis in 1850 (Swanson *et al.*, 1978) to determine the speed of nerve conduction. In 1912, Poffenberger compared stimulus perception/motor control in the same brain hemisphere to trials where the stimulus perception/motor control were in opposite brain hemispheres to estimate transmission time in the corpus callosum at about 4 ms (Swanson *et al.*, 1978). Berlucchi *et al.* (1971) confirmed this with their own estimate of 3 ms. The right hand and verbal responses are controlled by the left hemisphere. However, data from Filbey and Gazzaniga and Moscovitch and Catlin show a right-visual-field advantage does not exist with a verbal response (Swanson *et al.*, 1978). Swanson *et al.* (1978) concluded that simple response time is too variable to estimate transmission time of the corpus callosum.

2. Brain lesions

Ten trainees at the Spastics Society Industrial Rehabilitation Unit were diagnosed with early unilateral lesions, five on the left hemisphere and five (one female) on the right hemisphere. All other subjects (except as noted above) were male (Rees, 1971). Mean age was 18.4 years (range 16.9-23.4). The mean IQ was 86 (range 75 to 104). In the simple response time task there were two forms. In the "no-travel" condition, the subject rested his hand on the response bar. In the "travel" condition, the subject rested his hand on a Morse key until he saw the stimulus, and then moved his hand about 7 inches to the response bar. The preliminary interval was 1 to 2 s after a verbal "ready" was given. The left/right hand for response was randomized. In the no-travel condition, the response time for the affected hand (228.3 ms) was not significantly different that for the non-affected hand (219.6 ms). In the travel condition, the response time for the affected hand (628.1 ms) was significantly slower than for the non-affected hand (462.9 ms). The lack of significant difference in the no-travel condition indicates that early lesions may affect motor control more than recognition.

3. Measures of hearing in non-verbal children

Standard audiometric procedures are least reliable with children who manifest peripheral and central hearing defects (Davis and Goldstein, 1961), especially in children who are non-verbal with low motivation. Techniques involving measurement of autonomic responsivity have proved difficult to instrument with marked inter-individual and inter-laboratory differences in threshold assessment. Rapin and Steinherz (1970) reported that several researchers, Chocholle, Maspetiol, Sato and Matsukaki, have proposed measuring response time as an added dimension for clinical audiology.

Costa *et al.* (1964) tested the use of response time as a technique for assessing responsiveness to sound. 28 normal children (5 to 10 years age) responded more rapidly to paired stimuli than to either modality (visual or auditory) alone. A group of 40 children (5 to 10 years age) with communication disorders at a school for the deaf failed to respond more rapidly to paired stimuli versus visual stimuli. Positive reinforcement (M&M candy) improved response times in both groups. Sound alone, visual alone, and paired stimuli were intermingled during testing.

Rapin and Steinherz (1970) studied children (from 60 to 164 months) attending a school for the deaf. Four of 12 children initially unresponsive to sound learned to respond to sound. Rapid responses to light and light plus sound, and all responses to sound alone were rewarded with candy. Four children initially unresponsive to sound, learned to respond to sound during the study. The methods were similar to those in Costa *et al.* (1964) where 7 subjects learned to respond to sound. Response time curves gave objective information about efficiency and consistency of responses to supra-threshold sound stimuli, indicating validity of clinical audiometry. A marked increase in response time as stimulus intensity decreased, indicated a threshold within about 10 dB.

4. Effect of mental retardation

Work on the use of response times in assessing mentally retarded children appears as early as 1955 (Bradley *et al.*, 1955).

Response times of normal students were significantly ($p<0.01$) faster and less variable than mentally retarded students (IQ 45 to 70) in both choice and simple visual response time tasks. Subjects were matched for age, sex and race (Caffrey *et al.*, 1971). Gosling and Jenness (1974) found the response time of normal subjects (252 ms) were significantly faster than retarded subjects (386 ms). The effect of the

length of preliminary interval and the prior-preliminary was also greater for retarded subjects.

Ellis proposed that mentally retarded people have a stimulus-trace deficit (as described in Gosling and Jenness (1974)). The stimulus trace is an inferred temporary condition of the organism persisting briefly after the cessation of a stimulus and Ellis suggested that retarded people were deficit in this trace. This is hypothesized to account for short term memory and the ability of an organism to respond to a stimulus no longer present. Kohler used it to account for negative time error in psychophysics judgments; Pavlov to account for trace conditioning; Mowrer to explain delay of reinforcement effects; and Hull to explain generalization. The stimulus trace theory would predict less effect of prior-preliminary interval on response time in retarded subjects, which is contradicted in the study by Gosling and Jenness (1974).

An expectancy hypothesis suggests that when a critical feature of the trial is expected the response time is relatively fast; and when it is unexpected, the response time is relatively slow. If the subject used the prior-preliminary interval to estimate the current preliminary interval, then a short preliminary interval following a long preliminary interval resulted in a slower response time. A long preliminary interval following a short interval would also violate expectations, but the subject would then expect the stimulus "any millisecond now".

5. Loudness

Fletcher and Munson (1933) defined loudness as a psychological term used to describe the magnitude of an auditory sensation. Fletcher and Steinberg (1924) defined a mathematical formula for defining loudness, but it was limited to their data set. Fletcher developed a new formula in 1925. In the 1930s, the sectional committee on Acoustic Measurements and Terminology of the American Standards Association

proposed definitions for acoustical terms. These definitions were proposed by Fletcher and Munson (1933). Intensity in the direction of propagation is given by

$$J = P^2/pC \tag{1.3}$$

where J is in units of $(ergs/sec/\ cm^2)$.

Reference intensity level was 10^{-16} watts/cm^2. In a plane or spherical progressive sound wave in air, this intensity corresponds to a root mean square pressure of 0.000204 bar at 20 °C and a pressure of 76 cm Hg. Intensity level is the number of dB above the reference dB. A pure tone at 1 kHz will be used as the reference for loudness comparisons. A pure tone having a frequency of 1 kHz was chosen as the reference for loudness because (1) it simplifies math formulae, (2) it has a simple definition, (3) it was used as a reference for pitch, (4) there is large range from the threshold of hearing to the threshold of pain, and (5) 1 kHz is in the mid-range of audible frequencies for humans. A loudness level is measured by the intensity level of the equally loud reference tone and is expressed in dB.

Equal loudness curves are determined by asking human subjects to compare the loudness of a 1 kHz tone with a tone of a different frequency. The subject adjusts the amplitude of the comparison tone until he perceives the tone to be the same loudness as the 1 kHz tone. In this way the amplitude needed to produce the same loudness across various frequencies can be determined (see Figure 1). The loudness equivalent to a dB level at 1 kHz is termed a phon. So the loudness at 20 dB and 1 kHz is 20 phons and the amplitude needed for the subject to perceive the same loudness at another frequency is also 20 phons.

Equal latency curves are determined by finding the amplitude at each frequency that produces the same response time. An example for the house finch can be seen

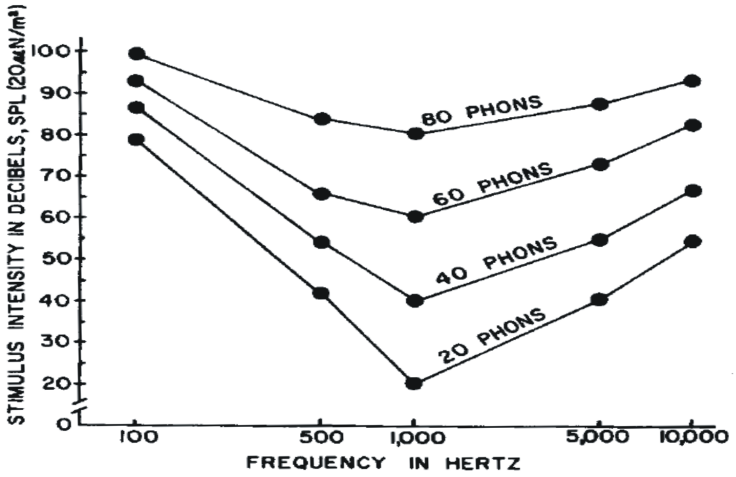

FIG. 1. A plot of the stimulus intensities needed to produce equal loudness across five stimulus frequencies across four human subjects. From Kohfeld *et al.* (1981).

in Figure 2. When equal loudness and equal latency curves have been calculated for the same subject (Pfingst *et al.*, 1975a; Kohfeld *et al.*, 1981) they tend to create similar, but non-identical contours (see Figure 3). Kohfeld found a greater change in response time from 20 to 40 phons at 1 kHz than at higher or lower frequencies. The relationship between phons and response time was more consistent (and more linear) at 60 and 80 phons.

6. Muscle function

Etnyre and Kinugasa (2002) compared the response time and response time components (pre-motor and motor) between normal and post contraction conditions. The response time, processing time and muscle contractions were faster following isometric contraction for a learned task than without the isometric contraction.

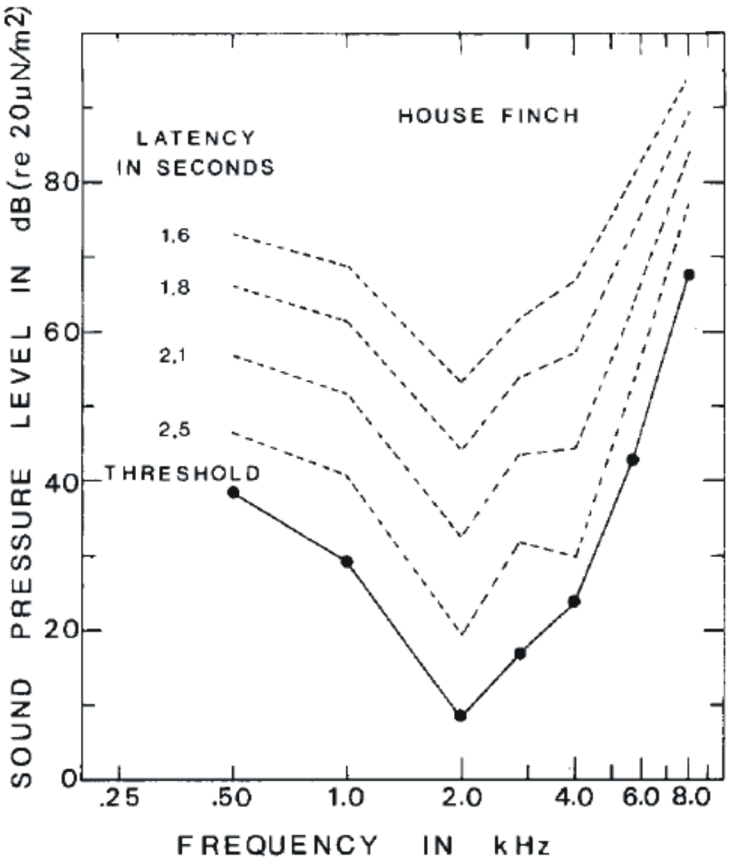

FIG. 2. Equal latency curves from the house finch derived from response time-intensity functions. From Dooling *et al.* (1978).

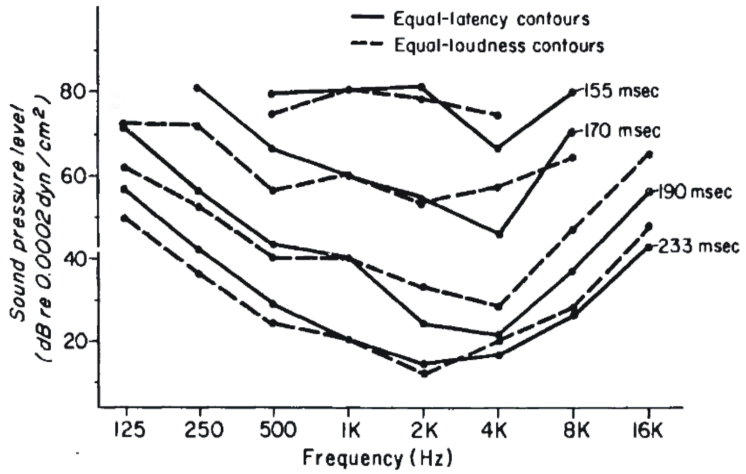

FIG. 3. Equal latency and equal loudness contours for two humans. Latencies from top to bottom were 155, 170, 190, 233, >1000 ms for H1 and 184, 2200, 235, 363 and >1000 ms for H2. Contours were calculated from latency-stimulus amplitude functions where N for each data point was 30. From Pfingst *et al.* (1975a).

7. Hearing aids

Pfingst *et al.* (1979) tested the functional aspects of a cochlear prosthesis in six male macaques (*M. mulatta* and *M. nemestrina*) ranging in age from 2.3 to 4.5 years. The macaques were trained to depress a key when a light came on and hold it for a random foreperiod, releasing the key at the onset of a tone. 1000 ms was the maximum response time. Response time varied systematically as a function of stimulus amplitude. Data was *not* pooled across subjects. Response time for one macaque was about 225 ms at 100 dB SPL for white noise in the non-implanted ear. Electrodes on the cochlear implant were stimulated electrically rather than with sound. They obtained similar results in studies with the same type of implants in humans.

H. Review of species in response time studies

While humans have been the subject of many or most response time studies, a number of other species have been studied. Only other vertebrate species have been examined.

1. Starlings (*Sturnus vulgaris*)

Startle response was examined in starlings (*Sturnus vulgaris*) in an anechoic chamber (Pomeroy and Heppner, 1977). Their interest was in how response time related to communication modes in flock movements. The start of a startle response began with flexor contractions which were detected via a piezoelectric crystal in contact with the perch. The mean response time of starlings (*Sturnus vulgaris*) to 1 ms 17,200 lx flash of unfiltered white (5600 k color temperature) light stimuli was 76.38 ms (13.23 ms sd). The mean response time to a 30 ms 2000 Hz 120 dB SPL pure tone (rise time 1.75 ms) burst was 80.64 ms (14.02) with a 45 dB ambient and white noise. The

response to visual stimuli was significantly faster by 4.3 ms (F=8.23, df=1,9) in a repeated measures analysis of variance (Anonymous, 1996). Data was pooled across subjects. Medians were plotted and represent at least 50 trials.

2. House finch (*Carpodacus mexicanus*)

Iso-latency contours for house finch (*Carpodacus mexicanus*) were determined for 1.6, 1.8, 2.1, and 2.5 s. The 1.6 s latency line was about 40 dB (re 20 μPa) above threshold at 1 kHz (Dooling *et al.*, 1978). Data was collected in a single walled sound deadening booth with ambient noise of 28 dBA re 20 μPa. Four house finches, two male and two female, were tested with 5 s duration tones with a 50 ms rise/fall time. The house finches were held in plastic tubes and trained to bite a response bar when they heard a tone to avoid a 0.1 mA electrical shock through wires wrapped around each leg. The subjects were trained until stable thresholds were obtained on each frequency. Seven frequencies were between 0.5 and 8.0 kHz were tested each day during the 10 days of data collection. Data was pooled across subjects to create an audiogram and equal latency curves for the house finch 2.

3. Pigeons (*Columba livia*)

Blough and Blough (1978) examined effects of luminance on response time in pigeons (*Columba livia*). The pigeons were dark adapted for 45 minutes prior to 384 trial sessions on most week days. White noise started a variable preliminary interval of 1 to 1.5 seconds. Inter-trial intervals of 20 seconds, with pecks in the last 2 seconds or during the preliminary interval delaying the next trial. The pigeons pecked an illuminated key. Responses when the key was lit turned off the light and activated the food hopper 1/8th of the time. Trials without a response ended after 2 seconds. The fastest response times ($\sim$550 ms) were to white light between 1 and 2 log

cd/m^2. Response time increased as luminance decreased to -3 and as it increased to 3 log cd/m^2. Increasing response time to increasing stimulus intensity is non-typical. Blough and Blough (1978) discusses two hypotheses for this result. Cone activity may inhibit responses attributable to rods, particularly in pigeons, since they have more cones in the peripheral retina. This cone/rod interaction may have slowed response times to bright lights. Alternatively, it is possible that the bright lights were aversive to pigeons.

4. Rat (*Rattus norvegicus*)

Stebbins and Lanson (1961) studied variability in response time in four yearling albino rats. The rats pressed a bar in response to a neon light ready signal and released the bar in response to a 4 kHz tone. A twenty second Inter-trial interval followed. If the bar was released, the light turned off and a 27 s timeout to the next trial was initiated. This procedure resulted in less variable response times than in earlier work (Stebbins *et al.*, 1960).

Stebbins (1962) measured response time in four 14-month old brown rats when they released a bar in response to a tone with a 0.15 ml of a 20% sucrose solution as a reward. After response times stabilized, animals were then tested using a 0% solution for two days. The subjects' behavior was re-stabilized on 20% solution and then tested on 5% solution for two days. Both response time and variability of response time increased with decreasing concentrations of sucrose.

Stebbins and Lanson (1962) studied response times in four 8-month old brown rats. The foreperiod (preliminary interval) was variable between 0.05 to 3.0 s with a mean of 1.5 s. Reinforcement schedules varied from 9% (1/11) to 100% of the trials. With higher percentages of trials reinforced, the median response times became faster and less variable. Stebbins (1962) and Stebbins and Lanson (1962) suggest that

response time is inversely related to reinforcement.

Moody (1969) determined equal brightness functions for seven rats. A trial began with the rat pressing and holding a response level in response to a ready signal of white noise. After a variable foreperiod (or preliminary interval) from 0.2 to 3.0 s, the visual stimulus under examination was presented. Bar releases within 1 s in the presence of the second stimuli were rewarded with water. The test stimulus was one of 16 wavelengths of monochromatic light from 433 to 670 nm and the amplitude varied over a 4 log unit scale at each wavelengths. Pressing the lever before the ready signal or the test tone ended the trial with a timeout. Each day's session consisted of 80 trials of which the first 8 were designated as warm up trials. There were 8 catch (no stimulus) trials. 64 latency data points were used from 64 days of testing for 32 observations at each of 8 intensities of 16 wavelengths.

Variability increased as median latency increased (hence as amplitude decreased). Moody calculated equal latency for 550, 600, and 700 ms. In general, high amplitude light was needed at longer wavelengths to produce the same latency. The curves are roughly parallel to that for scotopic spectral sensitivity for rats.

5. Chinchilla (*Chinchilla laniger*)

Young (1980) looked at reaction times in chinchilla (*Chinchilla laniger*) in an Industrial Acoustics Model 400a chamber. The chinchilla pressed a nose key when a light came on. At a variable time later (centered on 0.5 s) a tone started, and a release of the button within 1024 ms resulted in food pellets being presented to the subject. Pre-tone releases turned the light off and cancelled the trial. On "catch" trials, food was delivered when the subject continued to depress the key for 1024 ms. The Inter-trial interval was from 5 to 8 s. Initial training and the first test frequency was 4 kHz. There were 9 stimulus levels. The median of 50 response times at each

level was used. 4 kHz testing was repeated every 3 weeks. There was variation within each subject across weeks of testing at 4 kHz. The last two of the five data sets for 4 kHz were more consistent with each other than with the first two. There may be increased stability with practice. The response time to well above threshold stimuli in the last 4 kHz data set for each subject ranged from 550 to 650 ms. Consistent with the suggestion of response time as a reciprocal of loudness (Aikin, 1974), exponential decay curves were fit to the data of the form $y = ax^{(-b)} + c$.

6. Rhesus monkeys (*Macaca mulatta*)

Rhesus monkeys (*Macaca mulatta*) in a yes/no experiment responded fastest when correct to signal plus noise (Sn) stimuli. Stimulus amplitude was referenced to 45 dB SPL. With a 1 dB increase in signal, the subjects responded between 375 and 475 ms depending on probability of signal presence. With a 3 dB increase in signal, the subjects responded between 250 and 300 ms depending on the probability of signal presence (Clopton, 1972). In both cases, initial noise background level was -85 dB with a uniform spectral intensity from 0.5 to 16 kHz. Data was *not* pooled across subjects.

Response times to suprathreshold sounds were studied in rhesus monkeys (*Macca mulatta*) and humans in the same study using the same data collection methods (Pfingst *et al.*, 1975a). Depression of a response key in the presence of a light produced a randomly variable foreperiod of 0.4 to 4.5 seconds followed by the onset of a tone. Key release during the tone stopped the tone and light signal and produced a reinforcement (0.2 ml of applesauce for the monkey and a light for the human). The next trial began after a 1 second no-response interval. The tone remained on for a maximum of 1 s and if no release occurred during the 1 s, the light and tone ended, ending the trial without reinforcement. Humans (H) were told to release as

quickly as possible. The monkeys (M) were shaped for quick release by a differential reinforcement of brief latency responses (Miller and Glickstein, 1966). A 7 s "time-out" was used for releases before the onset of the tone. Releases occurring less than 100 ms after tone onset were not reinforced. Response times plotted are median response times for at n=50 data points. Data was *not* pooled across subjects. Variability of RT and RT itself were decreased as stimulus amplitude increased. Equal latency curves were constructed. The slope of the RT-amplitude function decreased at higher amplitudes. Subject M2 responded to 20, 40, 60 and 80 dB 1000 kHz tones at 486, 368, 319 and 290 ms respectively. H1 responded to 20, 40, 60 and 80 dB 1000 Hz tones at 233, 190, 170 and 155 ms respectively. H2 responded to 20, 40, 60 and 80 dB 1000 Hz tones at 363, 235, 200 and 184 ms respectively. So the humans responded faster than the rhesus monkeys. They used an N=30 for each data point.

Pfingst *et al.* (1975b) determined threshold for humans and rhesus monkeys and obtained thresholds similar to those in the literature and with the same subjects using forced choice for the monkeys and a clinical hearing test for the humans. The RT thresholds appeared to be slightly lower than the clinical audiograms by 2.6 dB (re 20 μPa) on average. RT thresholds were computed based on 100 ms $<$ RT $<$1000 ms based on 20 to 30 trials at each frequency-intensity combination. Thresholds were defined as halfway between the guess rate (based on false positives in catch trials) and 100% correct. The clinical tests used ascending limits and the timing of the presentation of the stimulus was controlled by the tester with no input from the subject. So the subject may have been less "prepared".

7. Pigtail macaques (*Macaca nemestrina*)

Pigtail macaques (*Macaca nemestrina*) were trained to release a key at the onset of a 1 kHz tone or visual (light) stimulus. In general, the latency of the response was

inversely related to the intensity of the stimulus. The subject was rewarded with food. There was greater variability in the latency to low intensities (Stebbins and Miller, 1964). Well above threshold response times to the light were about 310 ms for one animal. For another animal, the response time to the light and to the tone was about 390 ms and 300 ms respectively. N=80 for each stimulus type and intensity. Data was *not* pooled across subjects. Romba *et al.* (1963) obtained similar results with a 2 kHz tone using key-press and shock avoidance. Variability in response time was greatest at lower stimulus amplitudes. The subjects responded faster and with less variability when a time limit on rewarded response was in effect. A 400 ms limit produced slightly faster responses than a 500 ms limit.

8. Crab-eating macaques (*Macaca irus*)

Two male crab-eating macaques (*Macaca irus*) were trained to release a key at the onset of a pure tone after a variable foreperiod of 1 to 4 sec (Stebbins, 1966). Response time was measured for 6 frequencies from 250 Hz to 15 kHz over a 70 dB re 20 μPa range. Equal latency curves were constructed. Peak sensitivity was near 1 kHz. There were 60 trials at each frequency-amplitude combination. The median well above threshold response time for M1 was about 200 ms at 1 kHz and 100 ms duration. Both response time and variance decreased with increasing stimulus amplitude from 25 to 95 dB re 0.0002 dyn/cm^2). Data was *not* pooled across subjects. The author suggested a new unit called *louts* based on loudness and latency, where one lout = 10,000 * 1/L and L is latency in ms).

Macaca irus were tested at 250 Hz and 8 kHz. Response times to 60 dB re 0.0002 dyne/cm^2 were 270 and 280 ms respectively. However, the slope was steeper here than for the squirrel monkey and response times at 90 dB were about 230 ms for both frequencies for animal M10. Data was *not* pooled across individuals (Miller

et al., 1969). Monkeys were trained to press down on a key at the onset of a light, hold the key down for a variable period of 1 to 4 seconds and release the key on the onset of a pure tone.

9. Squirrel monkey (*Saimiri sciureus*)

Iso-latency contours for the squirrel monkey (*Saimiri sciureus*) were determined for 300, 330, 400 and 500 ms tonal stimuli. Thresholds and iso-latency curves were determined for stimuli from 0.125 to 46 kHz. Data was kept separate for individuals (Green, 1975). Response time to stimuli at 1 kHz well above threshold (60 dB re 0.0002 dyne/cm^2) was about 260 ms. Green (1975) looked at response times and audiograms using two experiments. In one, the animal responded to avoid receiving an electric shock. In the other, the animal responded to receive a food reward. No difference was found between auditory threshold functions obtained with an aversive stimulus and those obtained with an appetitive stimulus.

10. Bottlenose dolphins (*Tursiops truncatus*)

There are two previous studies reporting response times of marine mammals (Ridgway *et al.*, 1991, 2001). Ridgway *et al.* (1991) is an abstract of a conference presentation that reports response times for seven bottlenose dolphins (*Tursiops truncatus*) as subjects. Acoustic stimuli varied in frequency, duration, and amplitude. Subjects gave an acoustic response (AR) to stimuli. The response time was taken from a digitized recording of each trial. The range of median response times was given as 145 to 300 ms for simple response times, and as 170 to 448 ms for choice response times. Detailed results from the simple response time data taken in this study are given in chapter II.

11. White whales (*Delphinapterus leucas*)

Ridgway *et al.* (2001) examined the hearing of white whales (*Delphinapterus leucas*) at 5, 100, 200 and 300 m depth. The two subjects (NOC & MUK) responded to 500 ms tones in a method of free response for up to 12 minutes using a modified staircase method. Hearing threshold remained the same at all depths. Response times were used as another method of testing for differences in hearing in white whales between the surface and at depth. Subjects emitted a whistle in response to perceived stimuli. Response times were taken from digitized recordings of each trial. No significant differences in response times were noted as an effect of depth. Response times were noted as being slower near threshold than well above threshold. Mean near threshold response times for 20 whistle responses from each subject at each depth tested were presented. The female subject (MUK) had mean response times from 861 to 953 ms. The male subject (NOC) had mean response times from 808 to 870 ms. The response times were not significantly different at the various depths for either subject.

I. Natural history of bottlenose dolphins and white whales

There are 80 species of whales, dolphins, and porpoises in the suborder Odontoceti of the order Cetacea ranging in adult size from less than 2 m to over 14 m (Ridgway, 1997). They live in all oceans with four species that live only in fresh water. The suborder Odontoceti, toothed whales, includes superfamilies: Plantanistoidea, river dolphins; Delphinoidea, dolphins; Ziphioidea, beaked whales; and Physeteroidea, including sperm whales. The Delphinoidea include over half of all cetaceans with 42 species. The family Monodontinae consists of three species including Delphinapterus, the *beluga* or white whale. The Delphinidae is the largest family in this suborder and includes 33 species. *Tursiops truncatus* is in this group and is distributed worldwide.

Bottlenose dolphins have coastal and offshore forms in all places they have been studied (Leatherwood and Reeves, 1983). *Tursiops truncatus* are found in temperate and tropical waters on both sides of the equator and as far north as Scandinavia, Nova Scotia and northern Japan, and as far south as Australia, Chile and the tip of South Africa (Leatherwood and Reeves, 1983). They grow up to 3.9 m in length and 275 kg in mass. Typically they have from 18 to 26 teeth in each row. *Tursiops truncatus* tend to live in larger groups (from less 25 to groups of several hundred) off shore or in open waters compared to smaller groups (around 10 or less) inshore, within barrier islands or marshes (Shane, 1977; Wells *et al.*, 1980; Leatherwood and Reeves, 1983). Coastal bottlenose dolphins of southern Argentina primarily stayed in water less than 6 m deep during the summer months (Würsig and Würsig, 1977; Würsig, 1978)

Males reach sexual maturity at about 11 years and females between 5 and 12 years. Calves nurse for a year or more. Predators include killer whales and sharks. Bottlenose dolphins have been observed actively avoiding sharks. More than 6 percent of all captured dolphins in the Sarasota, Florida have scars from shark bites (Wells *et al.*, 1980).

Tursiops truncatus has been observed eating a wide variety of prey using many specialized foraging techniques. Cooperative herding methods have been observed when bottlenose dolphins feed on schooling fish. Individual feeding has been observed on benthic and reef dwelling fish. Feeding seems to peak in early morning and late afternoon in the well studied group near Sarasota Florida. The stomach contents of 16 stranded dolphin consisted entirely of fish (more than 15 species) most of which were more or less associated with sea grasses (Barros and Wells, 1998). The major species were soniferous, and may have been located by passive listening. Stomach contents of animals that stranded on nearby open Gulf beaches included cephalopods

in 21% of the strandings.

Bottlenose dolphins forage in spartina marshes in Georgia by herding fish into mud flats and beaching to pick up the fish with biting movements while sliding back into the water (Hoese, 1971). This method is primarily used in spring and fall. In summer, this method is used within 30 minutes of low tide.

Heithaus and Dill (2002) examined the effects of food distribution and predation risk by tiger sharks (*Galeocerdo cuvier*) on the distribution of bottlenose dolphins in Sharkbay Australia from 1997 to 1999. Tiger sharks were abundant in the warm months and absent in the cold months of 1997 and 1998. When present, sharks were found primarily in shallow sea grass habitats where they were difficult to detect either visually or with biosonar. Dolphin prey biomass was significantly greater in shallow water than deep water and did not vary seasonally. The distribution of foraging dolphins matched prey distribution when sharks were absent. During the warmer months when sharks were present, there were fewer dolphins in shallow water than expected based on prey distribution. Groups were larger in more dangerous, but more productive shallow water. Group size was also larger during resting and resting occurred in deeper water. Apparently distribution of tiger sharks affects bottlenose dolphin use of habitat for both foraging and resting.

White whales (*Delphinapterus leucas*) reach a length of about 4.5 m and 1500 kg. White whales are confined to arctic and subarctic waters. A trait of *Delphinapterus leucas* is that they can turn and nod their head due to the free cervical vertebrae, which is uncommon in cetaceans. Instead of a dorsal fin, the white whale has a narrow ridge along the spine just behind the midpoint of the back. There are about 8 to 11 teeth in each upper jaw and about nine in each lower jaw. White whales have been seen in groups of more than a thousand animals, particularly in estuaries in the summer. Females probably become fertile at about five years of age and males at eight

or nine years. White whales are hunted by killer whales, polar bears, and occasionally walrus. Humans have hunted white whales for both subsistence and commercial use (Leatherwood and Reeves, 1983).

The breeding season is in May, followed by a 14.5 month gestation and single births. Lactation lasts about 2 years for a 3 year reproductive cycle. The females and newborns seem to favor shallow water areas. White whales are often seen in shallow water, but use deep water as well (Leatherwood and Reeves, 1983). White whales have been studied relative to both the subsistence and the commercial harvest. The most accessible area for observing this species is where the Saguenay River empties into the St. Lawrence.

The smallest white whales live in Hudson Bay and the White Sea and the largest are found off Greenland and the Okhotsk Sea (Brodie, 1989). The longest migration is between summers in Mackenzie and winter in the central Bering Sea (Brodie, 1989). Stocks in near-shore summer habitat appear to be discrete breeding groups although some may overwinter in common feeding areas offshore. About 10,000 individuals, or about a third of North America's population, live in Hudson Bay (Watts and Draper, 1988). Adult white whales are more abundant in warm water estuaries during the summer calving seasons. There is a lack of evidence of births in the warmer waters, and neonates have been observed offshore. Stomach contents of harvested animals indicate that the estuaries are not an important source of food (Sergeant and Brodie, 1973) and a few harvested animals have full term neonates (Finley *et al.*, 1982). Watts and Draper (1988) speculated that molting may be a factor in use of warm water.

Satellite dive records from six white whales (Heide-Jorgensen *et al.*, 1998) show vertical speeds of 0.5 to 1.9 m/s for depths of 52 to 80 m. Most dives lasted either less one minute or from 9 to 18 minutes. Mean maximum daily dives were from 483 to 665 m. The deepest recorded dive was 872 m. Smaller whales made more dives and spent

more time at the surface. The maximum depths of dives were near the maximum sea bed depth. Females dove more between 2300 and 0500 hours than during other 6 hour periods. There was a difference in dive rates by time of day for males.

Natural predators include killer whales, polar bears and occasionally walrus. Polar bears seem to primarily capture whales migrating through narrow channels or entrapped in ice (Brodie, 1989). White whales seem somewhat prone to ice entrapment. White whales are able to swim in water depths that barely cover them. This can be used to escape killer whales (*Orcinus orca*) and extends feeding into shallow estuaries.

Summer food includes molluscs, annelids, fish, decapods, and large zooplankton. Weaning calves appear to feed on benthic organisms using suction (Brodie, 1989). Seaman *et al.* (1982) found that white whales off western Alaska preyed upon all species eaten by other marine mammals and taken by commercial fisheries. Watts and Draper (1986) observed a white whale, swimming on its side beneath a shoal of capelin (*Mallotus villosus*), executing tight circles or half circles with frequent changes of direction and ingesting capelin. Ridgway and Carder (1998) observed the two white whales employed in this study (MUK and NOC) using the nets of their enclosure to trap and consume anchovies.

Mature males are found in separate pods of 8 to 16 individuals and nursery groups comprise several adult females and calves. During migration, single older animals move in advance of the herd and attempt narrow passages between ice first. In Soviet waters, all-male aggregations of up to 500 animals have been observed with smaller mixed aggregations of up to 200. White whales are one of the most vocal odontocetes with the nickname of “sea canary” (Schevill and Lawrence, 1949).

J. Cetacean hearing and biosonar

Hearing has been studied in 8 of the 80 species of cetaceans, of those 7 species were delphinoids. I will summarize hearing studies on the two species of interest here, *Tursiops truncatus* and *Delphinapterus leucas*.

Johnson (1967) determined a behavioral audiogram for an approximately 8 or 9 year old bottlenose dolphin (*Tursiops truncatus*), Salty, in wooden circular tanks 8.2 m in diameter and 1.3 m depth. A stall-like enclosure was constructed of redwood and lined with rubberized horse and pig hair to reduce sound reflections. Hearing thresholds were determined using discrete trials and the animal responded by pressing paddle B within 12 seconds of the start of a 3 second test tone. Threshold was determined using an up-down staircase method of stimulus presentation.

Three subjects were tested to look at low frequency underwater hearing in *Delphinapterus leucas* (Awbrey *et al.*, 1988). The test pool was 13 x 13 x 4 m. The adult male in this study was one of the animals tested by White, Jr. *et al.* (1978). The speakers were suspended in-air 1.9 m above the subject's station. A variant of the ascending form of the method of limits was used to test seven frequencies from 125 Hz to 8 kHz with 500 ms tones. The animal stayed on station 0.5 m below the surface until it heard the test signal or was called back with a trainer's whistle. The thresholds observed agree with work by White, Jr. *et al.* (1978).

A two year old female *Delphinapterus leucas* was tested in San Diego Bay (Johnson *et al.*, 1989). The subject was trained to station on a bite plate 1 m below the surface. The animal responded to a tone by pushing the bite plate forward 15 cm to touch the disk with the bite plate. An in air speaker was used for frequencies below 1 kHz. Underwater hydrophones were used for frequencies above 1 kHz. Thresholds were measured at 32 frequencies between 40 Hz and 125 kHz. Thresholds between 5

and 100 kHz were masked by bay noise. Results were in reasonable agreement with those done by White, Jr. *et al.* (1978) and Awbrey *et al.* (1988).

Ridgway *et al.* (2001) examined the hearing of *Delphinapterus leucas* in the open ocean at 5, 100, 200 and 300 m depth. The two subjects (NOC and MUK) responded to 500 ms tones in a method of free response for up to 12 minutes using a modified staircase method of stimulus presentation. Hearing thresholds remained the same at depth.

White, Jr. *et al.* (1978) reported that the maximum sensitivity for white whales was at 30 kHz. Other frequencies with thresholds below 40 dB re 1 μPa were at 42.5, 60, and 85 kHz. These frequencies are near the peak frequencies for white whale echolocation clicks reported by Gurevich and Evans (1964). Johnson (1967) reported that the frequency with maximum underwater hearing sensitivity for the bottlenose dolphin was at 50 kHz (45 dB re 1 μPa). Critical ratio is the ratio of signal power to noise spectrum levels at masked threshold. A low critical ratio suggests good frequency discrimination ability. Johnson *et al.* (1989) reported critical ratios for white whales about 3 dB lower than the critical ratios for *T. truncatus* reported by Moore and Au (1982).

The major axis of the white whale biosonar beam is 5 degrees above the plane defined by the animal's teeth with a 3 dB beamwidth of about 6.5 degrees in both the vertical and horizontal plane (Au *et al.*, 1987) and with an directivity index of 32.1 dB (Au, 1980). The beamwidth of the bottlenose dolphin is about 11.7 degrees in the vertical plane and 10.7 degrees in the horizontal plane (Au, 1980). The directivity index is about 26.5 dB (Au *et al.*, 1984).

Tursiops truncatus produced biosonar signals with peak frequencies of 120 to 130 kHz in Kaneohe Bay compared to 30 to 60 kHz in a pool. The signals were 30 dB higher in Kaneohe Bay, which has a high level of snapping shrimp noise (Au

et al., 1974). In Kaneohe Bay, a white whale produced biosonar signals with peak frequencies of 100 to 120 kHz and 3 dB bandwidths between 30 and 40 kHz compared to peak frequencies of 40 to 60 kHz with bandwidths between 15 and 25 kHz in San Diego Bay. Signal amplitudes were about 18 dB higher in Kaneohe Bay than in San Diego Bay (Au *et al.*, 1985).

White whales matched performance with bottlenose dolphins on a target detection task in noise levels 8 to 13 dB higher. Turl *et al.* (1987) compared the mean maximum source energy flux density (E_e). At a 75% correct response threshold, the $(E_e/N_o)_{max}$ was approximately 1.0 dB for the *D. leucas* at three target differences and about 10 dB for *T. truncatus*. White whales have been observed in an experimental setting to use surface-reflected propagation paths (Penner *et al.*, 1986) to help avoid noise from a point source, perhaps explaining part of their superior performance in noise.

D. leucas was able to detect targets in clutter with a lower echolocation-to-reverberation ratios than *T. truncatus* (Au and Turl, 1983; Turl, 1990). This suggests that *D. leucas* can detect targets in 3.6 and 5.4 dB more reverberation than *T. truncatus*. *T. truncatus* and *D. leucas* appear to have about the same target detection range (Au, 1980; Turl, 1990).

White whales sometimes emit biosonar clicks whose interclick intervals are less than the two-way travel time (Turl and Penner, 1989). This is sometimes done in packets with time between packets greater than the two-way travel time. In other click trains, all or most of the interclick intervals are greater than two-way travel time (Turl *et al.*, 1987). Bottlenose dolphin biosonar clicks typically have interclick intervals greater than the two-way travel time so the echo return is during the interclick interval (Penner and Kadane, 1980).

White whales could discriminate polyvinyl chloride (PVC) targets 3.0 x 3.0 cm compared to 2.9 x 2.9 cm section on complex targets that were otherwise identical at 81%. A bottlenose dolphin comparing similar targets had chance levels of performance comparing sections 2.7 x 2.7 cm to those 3.0 x 3.0 cm (Gurevich and Evans, 1964).

White whale biosonar has better performance than bottlenose dolphins in detecting targets in clutter, targets in noise, and in some target discrimination tasks. White whale and bottlenose dolphin hearing sensitivity differs, as do parameters of their biosonar signals. These differences might relate to the white whales's adaptation to the arctic environment and ice.

Two series of studies at the US Navy Marine Mammal Program utilized many of the same subjects as in the research reported here. In one, the existence of age-related hearing deficits was examined. In the other, the response of dolphins and white whales to high-amplitude stimuli was examined. The data from this latter study was the same data set used to determine simple response times for near-threshold stimuli.

Eight bottlenose were trained to respond to 100 ms tones (Ridgway and Carder, 1997). Three male dolphins (ages 23, 26 and 34) exhibited a hearing deficit at four higher frequencies of 70, 80, 100, and 120 kHz even at 111-135 dB re 1 μPa. Three females (ages 11, 32 and 35) and one male responded to all frequencies. One female (aged 33) responded to all tones 80 kHz and below, but failed to respond to tones at 100 and 120 kHz. All males over 23 years showed some deficit in responding to tones of 60 kHz and higher frequency. Ridgway and Carder (1997) cites Ries as showing that a high percentage of humans (males more than females) show some high frequency hearing loss with age, so high frequency hearing loss with age in other species is not unreasonable.

In order to assess the possible effects of high amplitude sound on marine mammals, a study to determine temporary threshold shift was performed by the US Navy

Marine Mammal Program on subjects of both *Tursiops truncatus* and *Delphinapterus leucas*. When a subject is exposed to a high amplitude sound, there is the potential for a reduction in hearing sensitivity following the exposure. Such an observed reduction in sensitivity with a subsequent recovery of full hearing sensitivity is a *temporary threshold shift*. Sound exposure that reduces hearing sensitivity but is not recovered is termed *permanent threshold shift*. Finding exposures that cause temporary threshold shift gives information about sound exposure levels that are potentially harmful to hearing. The multi-year effort has resulted in several papers describing the experiments (Ridgway *et al.*, 1997; Finneran *et al.*, 1999, 2000; Schlundt *et al.*, 2000; Finneran *et al.*, 2002b). In order to obtain information on temporary threshold shift, baseline data on hearing thresholds had be obtained as a matter of course.

The purpose of the main project was to study temporary threshold shift which required repeated hearing threshold tests. I was able to collect response time data during these hearing tests. My analysis does not address effects of exposure to high amplitude sounds.

The two projects in this dissertation will characterize and compare response times in bottlenose dolphins (*Tursiops truncatus*) and white whales (*Delphinapterus leucas*) well above threshold in a listening task and as part of hearing threshold tests.

CHAPTER II

SIMPLE RESPONSE TIME IN A LISTENING TASK TO TONES WELL ABOVE THRESHOLD

A. Introduction

Measurement of response times in subjects can be broadly divided into two different approaches. When a subject has a single response behavior that indicates that it perceives a stimulus, the result is a *simple response time* (SRT). When the subject must choose which of two or more responses to give to a stimulus, the result is a *choice response time* (CRT). While the literature for simple response time in humans and laboratory animals (monkeys, rodents, birds) is ample (Cattell, 1886a; Bellis, 1931; Birren and Botwinick, 1955; Costa *et al.*, 1964; Botwinick and Thompson, 1966; Berlucchi *et al.*, 1971; Caffrey *et al.*, 1971; Blough and Blough, 1978; Dooling *et al.*, 1978; Braun *et al.*, 1996; Etnyre and Kinugasa, 2002), little has been reported so far with respect to response times in marine mammals (Ridgway *et al.*, 1991, 2001).

Simple reaction time studies have varied on the parameters of stimuli presented, on the means by which subjects respond to stimuli, and environmental conditions during testing. These factors are under the control of the experimenter. In studies of simple response time for acoustic stimuli, the experimenter can decide whether pulses, tones, tone contours, or words will be presented; the duration of stimuli; the amplitude of stimuli; and the frequency of stimuli. Subjects can be directed or trained to respond using an emitted audible response (very rarely even in humans) or with some movement or behavior pattern such as pressing a paddle or pecking a key. Many additional environmental factors may be controlled (or not) by the experimenter. All of these may have an effect upon the results obtained.

In most human simple reaction time studies, subjects respond to lights, pictures,

or tones by movement of some form of switch with a finger. Netsell and Billie (1974) looked at vocal response times for humans to the offset of a tone. The response was one of the following words, "pap", "bap" or "map", with a mean response time of 200 ms. The time between stimulus offset and start of EMG activity, the neural response time, was about 140 ms. The time from start of EMG activity to rise in the intraoral air pressure, mechanical response time, was about 60 ms. The speech reaction time to an above-threshold, easily-heard tone of about 200 ms (Netsell and Billie, 1974) was about the same as the finger reaction time reported in similar studies (Botwinick and Thompson, 1966; Luschei *et al.*, 1967).

While many parameters of stimuli may be manipulated experimentally, most simple response time work with animals has looked mainly at the effect of change in intensity or amplitude (Stebbins, 1990; Ridgway *et al.*, 2001).

Some speculated that increasing stimulus duration would have the same effect as increasing amplitude. By 1913, it had already been established that reaction time was inversely related to stimulus amplitude. The earliest person to experiment on the effects of duration on reaction time was Sven Froeberg. He looked at duration in visual stimuli with duration of 48, 24, 12, 6 and 3 ms. Froeberg concluded that reaction time increased by approximately equal arithmetical increments as the duration of the stimulus decreased geometrically. This held over a limited range. The increase in reaction time became more rapid as threshold was approached.

Wells (1913) also examined the effect of stimulus duration (between 12 and 1000 ms) on reaction time in humans. There was no evidence of increase in reaction time with decrease in duration. There was some trend to support the relationship that longer stimulus durations resulted in longer reaction times.

Several researchers have found that response time increased with age (Birren and Botwinick, 1955; Weiss, 1965). However, Bellis (1931) found that when comparing decade groups of humans (<=10, 11-20, 21-30 years), reaction time to either light or sound decreased with age. Reaction time did increase from the 10-30 age group through the 51-60 years age group.

B. Methods

Auditory response time data were collected on a time-available basis from 1986 to 1993 in San Diego Harbor, which has highly variable natural and man-made noise. Response time data were collected via a free response time method (Egan *et al.*, 1961) developed for dolphins and white whales by Ridgway and Carder (1997); Ridgway *et al.* (2001).

1. Subjects

Five Atlantic bottlenose dolphins (*Tursiops truncatus*) and two white whales (*Delphinapterus leucas*) ranging in age from 16 to 35 years participated as subjects in this study (Table I). The animals were housed in wooden floating pens (10 x 10 m to 13 x 25 m) with netting to form an enclosure located in San Diego Bay, California. All animals were kept in accordance with applicable federal regulations under constant veterinary supervision. All the experiments were conducted under a protocol approved by the Institutional Animal Care and Use Committee SPAWAR Systems Center San Diego, issued to Sam H. Ridgway and Donald A. Carder. The Center is accredited by the Association for Accreditation of Laboratory Animal Care. Diets included herring, mackerel, capelin, smelt, and squid in specific amounts to maintain a healthy weight relative to the animal's age, size and gender. Performance

TABLE I. Summary data on subjects for simple response time experiments.

Subject	Species	Sex	Weight (kg)	Length (cm)	Girth (cm)	Age	Begin Work	End Work	Est. Birth Year	Response to Tone	Response to Pulse
APR	*T. truncatus*	F	132.3	225	115	7	1991	1991	*1984	Whistle	
MAU	*T. truncatus*	M	229.1	260	242	32	1990	1992	1958	Whistle	
MAY	*T. truncatus*	M	185.9	258	132	15	1985	1991	1970	Pulse	
MUK	*D. leucas*	F	529.1	338	213	19	1986	1993	1967	Whistle	Pulse
NOC	*D. leucas*	M	596.4	384	198	11	1986	1987	1975	Pulse	Whistle
SLA	*T. truncatus*	F	208.2	261	134	25	1985	1993	1960	Pulse	
TOD	*T. truncatus*	F	218.6	266	135	32	1990	1992	1958	Pulse	

* Born at the Navy Facility

and number of work sessions per day did not affect the amount of food the animal received. At the time of the study, the subjects were healthy and not known to have any hearing loss at any of the tested frequencies. One subject, MUK, did have an elevated hearing threshold at 40 kHz relative to 30 and 45 kHz prior to the start of this work (Ridgway *et al.*, 2001).

Tursiops truncatus (Johnson, 1967) and *Delphinapterus leucas* (White, Jr. *et al.*, 1978; Awbrey *et al.*, 1988; Johnson *et al.*, 1989) have hearing ranges and sensitivities equivalent to or better than many marine mammals (Fay, 1988; Richardson *et al.*, 1995) based on behavioral audiograms (Figure 4). *Delphinapterus leucas* and *Tursiops truncatus* may be considered representative of many marine mammals for both broad bandwidth and high sensitivity that may be impacted by a wide range of anthropogenic underwater sound. Both species belong to the superfamily Delphinoidea, which includes over half of all odontocete cetaceans (Ridgway, 1997).

2. Equipment

In the original response time experiments (Ridgway *et al.*, 1991), data collection was performed via the use of digital computer equipment. Custom software controlled the shaping and presentation of acoustic stimuli and the subsequent analysis of data (Root, 1987).

A DEC PDP-11/24 computer running the DEC RT-11 operating system, DEC VT-240 terminal, DEC LXY-12 graphics printer, DEC RK-05 disk drive, and DEC LPS-11 Laboratory Interface Unit (LIU) comprised the computer equipment utilized. A Wavetek Model 154 Programmable Signal Generator and a prototype signal generator interface were used to generate acoustic signals under programmatic control. The DEC LPS-11 LIU provided digital control lines and analog-to-digital conversion capabilities. The trainer running a session used an SPST normally-open pushbutton

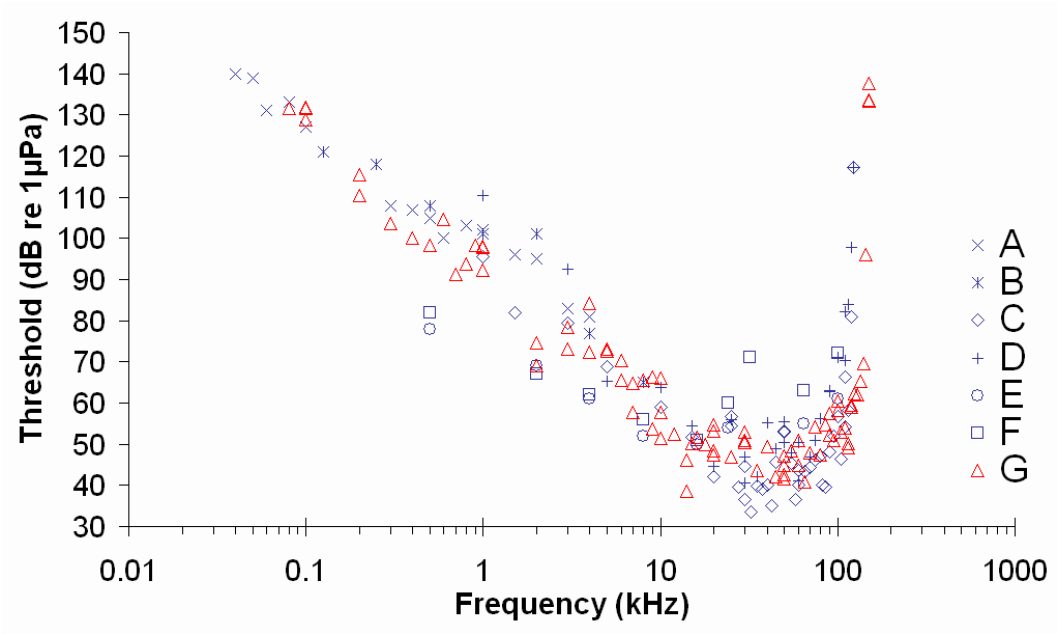

FIG. 4. Behavioral audiograms for *Tursiops truncatus* and *Delphinapterus leucas*. (A) *Delphinapterus leucas* from Johnson *et al.* (1989). (B) *Delphinapterus leucas* from Awbrey *et al.* (1988). (C)&(D) *Delphinapterus leucas* female and male from White, Jr. *et al.* (1978). (E)&(F) *Delphinapterus leucas* female and male in the open ocean from Ridgway *et al.* (2001). (G) *Tursiops truncatus* from Johnson (1967).

to request that a series of stimuli be presented by the software. The program would specify the acoustic signal to be sent. The signal was generated by the Wavetek 154 signal generator and projected via an LC-10 (higher frequency) or F42B (low frequency) projector. Audible responses by the subject were collected via a Brüel & Kjäer 8103 receiving hydrophone and Brüel & Kjäer 2635 charge amplifier (set for 40 dB gain), filtered with an Ithaco 4302 Dual 24 dB/octave filter. The responses were digitized by the LPS-11 unit and stored on the RL-02 disk drive for later review and analysis (Root, 1987).

The subject gripped a plastic bite plate on a polyvinyl chloride (PVC) framework at 1.0 m depth, keeping the head stationary. The projector hydrophone was positioned on PVC pipe approximately 1.0 m directly in front of the subject. The PVC provided a rigid structure to establish fixed relative positions between the subject and the projecting hydrophone with minimal distortion to the sound field (Johnson *et al.*, 1989). A listening hydrophone was positioned about 10 cm above and to the side of the blow hole to monitor whistle and pulse responses from the subjects.

The dolphins were presented with tone stimuli. Tones were ramped up and ramped down using a sinusoidal function over 2.7 ms. The whales were also presented pulsed stimuli. Pulse duration was 400 microseconds at 5 kHz and 500 microseconds at all other frequencies. (The shorter pulse duration at the lowest frequency, 5 kHz, was necessary to provide a sufficient number of stimulus cycles to accommodate the short ramp-up and ramp-down time.) Pulse repetition rate was 100 pulses per second to provide an inter-pulse interval of 9.5 ms.

Subjects were trained either to pulse or whistle to a tone or a pulsed stimulus as shown in Table I. To be included in the simple response time analysis, only tones or only pulses were presented on a given day. All stimuli in a given session were of the same type and the same duration. Stimulus frequency and/or amplitude was varied

within some data sets to compare multiple frequencies with single frequency series.

3. Procedures

Preparation for running a data collection session involved setup of the experimental apparatus, including the bite plate and projecting and receiving hydrophones. The custom software also required that a stimulus description file and stimulus sequence file be created. The stimulus description file specified various parameters of acoustic stimuli to be presented, including stimulus type (tone or pulse train), duration, frequency, and amplitude (Root, 1987). The stimulus sequence file specified some of the parameters for determining whether a response waveform was present in the recorded signal and also the number and sequence of stimuli to be presented based upon the stimulus description file.

A method of free response (MFR) (Egan *et al.*, 1961) was used during this listening task. In this method, the subject was presented with a series of brief tones with the time interval between tones pseudo-randomized. The interstimulus interval was from 1.1 to 2.1 seconds in 100 ms steps. The listening subject did not know the time of the next tone. The trained behavior of the listener was to respond when a tone was heard and to do nothing otherwise. In the study, the response was a whistle (Ridgway and Carder, 1997; Ridgway *et al.*, 2001).

A session started when the animal was brought into the testing enclosure and consisted of one or more "dives". The session ended when the animal was sent out of the testing enclosure. A dive or trial block began with the animal in front of the trainer, who signalled the subject to go down to the PVC test station 1 m underwater, and ended when the animal was given a buzzer "bridging stimulus" by the trainer signaling the animal to come up for air after responding to a series of test tones (Figure 5). For a data collection session, the subject was asked to hand station by a

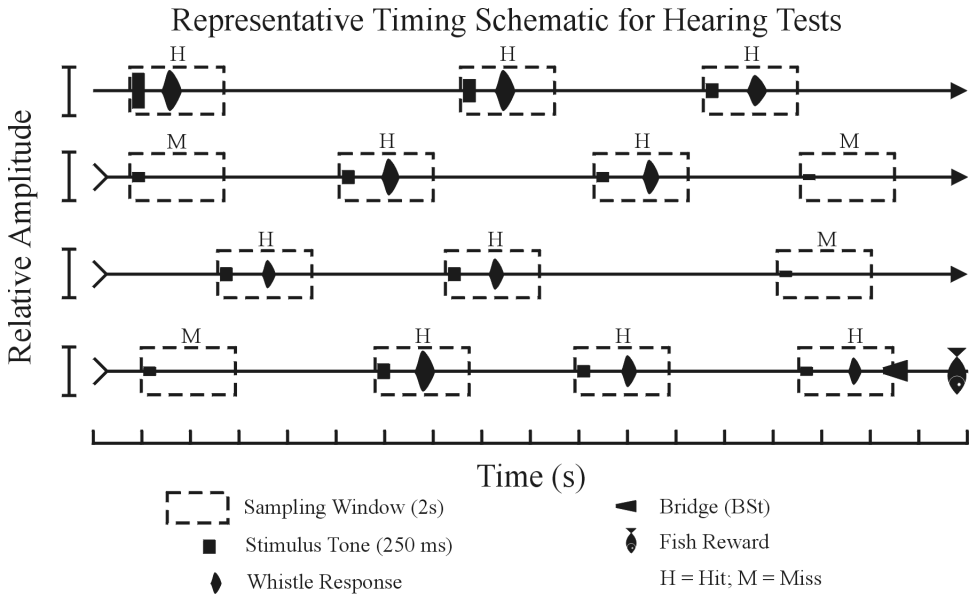

FIG. 5. Schematic of presentation of stimuli for *Tursiops truncatus* and *Delphinapterus leucas*.

trainer (rest their rostrum in the trainer's hand and await a cue), then given a cue to proceed to the bite plate. Once the subject was on the bite plate, the listening hydrophone was placed in position near the subject's blowhole. The trainer then would hold down the switch linked to the computer to begin the sequence of stimuli to be presented. The subject responded to each stimulus with a whistle vocalization. A period of 700 ms was recorded from the onset of the stimulus. The subject was given a *bridge stimulus* (a secondary reinforcing stimulus) for successful completion of the sequence of trials and given a food reward on return to a hand station. The subject performed one to several such sequences in a session. Occasionally, due to harbor noise or some other delay, there was a longer waiting period between dives. Normally, the waiting period between dives was determined by the trainer to give the animal a rest and allow the animal to refresh its respiratory gas balance.

4. Analysis

The digitized and stored response waveforms were edited by use of a custom program, R01 (Root, 1987). Each response waveform could be displayed and examined for any problems in noise level, ambiguity, or selection of onset of response time. The response could be accepted as is, the response time onset could be adjusted by the user, or the entire response excluded from the dataset. The R01 program produced a summary data file for each edited set of responses.

For analysis, data were divided into categories based on subject, data set, frequency, duration, and amplitude using the Microsoft "Excel" software package. Responses starting in less than 80 ms were extremely rare and were always more than 2 standard deviations from the mean response time; therefore these were discarded as too fast to be attributed to the stimulus and thus a false positive response. Since the recording window was limited to 1200 ms or less, only response times of less than that limit were recorded. Means and standard deviations were calculated on each of these combinations. Data points outside of the mean plus or minus two standard deviations were discarded as outliers. Linear regressions of the effect of stimulus amplitude on response time were calculated for each data set and tested for significance.

Further statistical analysis was performed using the Abacus Concepts "StatView" package. Response times were compared between species using a t-test. Response times were compared between individuals using analysis of variance. Least squares linear regression was used to examine the relationship between test tone amplitude and response time.

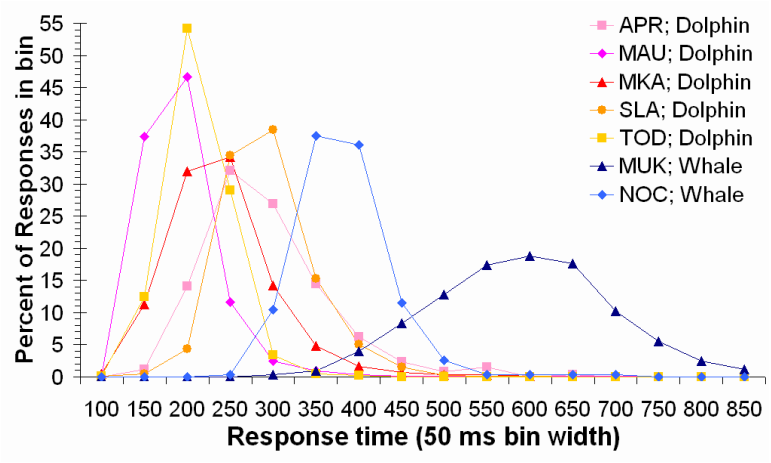

FIG. 6. Frequency polygon of response times for 120 dB stimuli at all frequencies and durations.

C. Results

During the 8 years of the study, over 77,000 responses were recorded and used for simple response time analysis. Figure 6 shows frequency polygons of response times for all frequencies and durations at 120 dB stimulus.

Responses to stimuli at all frequencies and durations at 120 dB were compared across subjects in an ANOVA on the basis of response time. Analysis of response time via ANOVA split by subjects shows significant differences at $p<0.0001$ (6 DF, $F = 21886.46$) as is shown in Figure 7. Using Fisher's *protected least significant differences* (PLSD), most between subject comparisons were significant at $p<0.0001$. The response time for APR, a young female born at the Navy facility, was not significantly different from that of SLA, a wild-caught male twenty years her senior. Comparison of response time by species using a *t*-test found that the dolphins (231.9 ms) were significantly faster than the whales (584.1 ms) at $p<0.0001$ ($t = -236.0$).

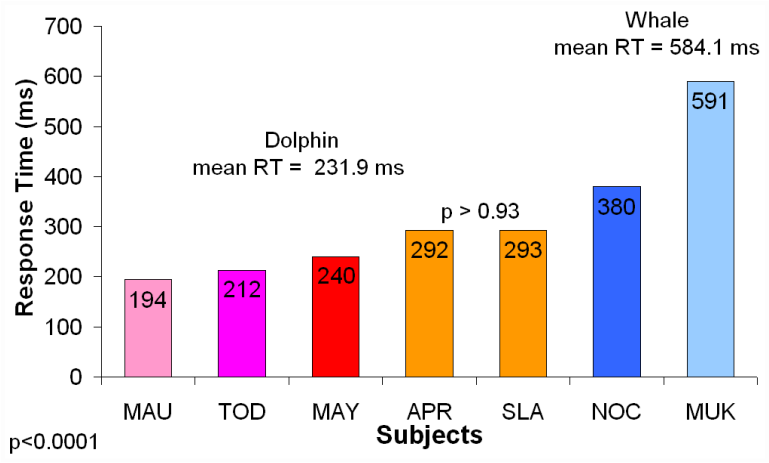

FIG. 7. Response times for all subjects. All between subject comparisons were significantly different ($p<0.0001$) except between APR and SLA ($p>0.93$). The whales (NOC and MUK) had significantly slower times than the dolphins.

Each distinct experimental condition will be referred to in the following text by a single-letter designation. An experimental condition comprises data taken with the same stimulus parameters in a single block of time.

1. Tests on dolphins

APR was available only for limited participation. The two data sets at 100 ms and 40 kHz show a fair amount of agreement in the relationship between response time and stimulus amplitude (Figure 8). There were three data sets that contained stimuli at 40 kHz, 100 ms and 120 dB. The response times were significantly different from each other (ANOVA $p<0.0001$, DF=2, F=10.272) with the slowest response in set C where multiple frequencies were presented all at the same amplitude.

The response time for MAU was greater at 60 kHz and above in three data sets, B, D and L (Figure 9). The rate of missed stimuli also increased at these frequencies, probably due to high-frequency hearing loss in this older male dolphin (Ridgway and

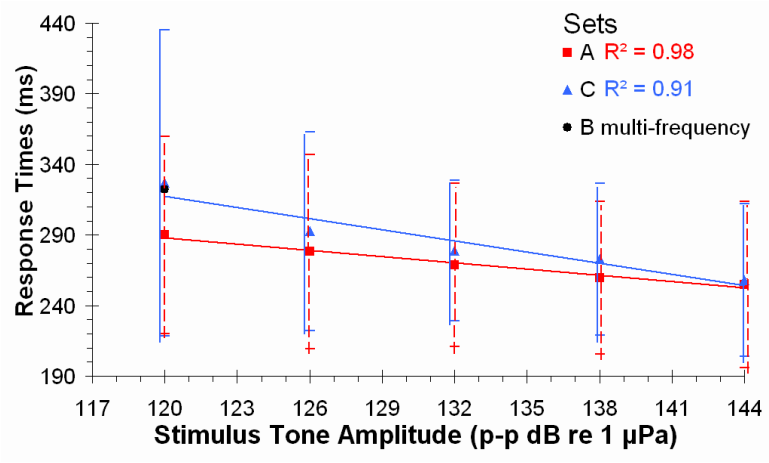

FIG. 8. Response times versus amplitude for APR for 100 ms stimuli and 40 kHz frequency.

Carder, 1997)(Table II). The relationship between stimulus amplitude and response time is shown in Figure 10. The slope is flatter at the lower frequencies where the responses are faster.

In 16 different data sets with varying duration and amplitude, response time for MAU showed an inverse relationship to stimulus amplitude. There was no strong relationship between duration and response time.

In eleven data sets at 100 ms and 40 kHz stimuli, response time showed an inverse relationship to stimulus amplitude (Figure 11). The training data set did not show this relationship and had slower responses. The next slowest response times were in an early data set with higher amplitude ambient noise. The two data sets with multiple frequencies and the first data set presented were the next slowest.

The response time for MAY was greater at 60 kHz and above in many of the data sets at different durations (Figure 12). The rate of missed stimuli also increased at these frequencies probably because of high-frequency hearing loss (Ridgway and

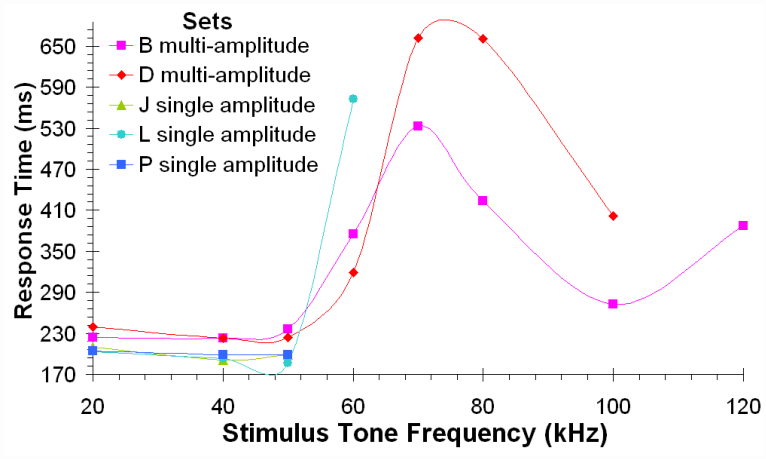

FIG. 9. Response times versus frequency for MAU for 100ms, 120 dB stimuli. Data sets J, L and P had only one amplitude. Data sets B and D had more than one amplitude, but only the responses to 120 dB stimuli are shown in this figure.

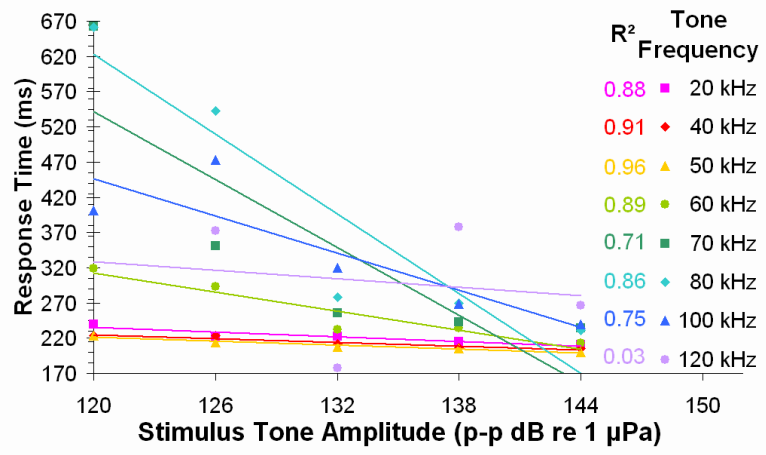

FIG. 10. Response times versus amplitude for MAU for data set D at 100 ms duration.

TABLE II. Percent hit for simple response time experiments.

	Subjects						
Frequency	APR	MAU	MAY	SLA	TOD	MUK	NOC
1 kHz						85.71	
2 kHz						77.78	
5 kHz			91.08	93.20	100.00	66.15	87.18
10 kHz			90.83	93.84	100.00	68.49	92.50
20 kHz	7.69	89.90	89.93	89.95	96.23	68.64	92.31
30 kHz			88.18	100.00		13.64	
40 kHz	79.34	95.61	90.08	87.84	91.81	0.22	
50 kHz	92.59	71.57	88.33	94.59	98.04	82.13	92.68
60 kHz	96.30	3.21	86.12	93.72	97.39	67.56	89.19
70 kHz	81.48	2.23	69.40	90.95	98.05	22.82	
80 kHz		5.78	20.34	54.12	97.49	65.40	89.19
100 kHz		4.17	16.67	3.27	98.68	62.98	88.89
120 kHz		2.80	23.08	4.95	93.62	24.27	88.89
Total	81.48	69.69	84.23	67.26	93.93	53.35	90.16

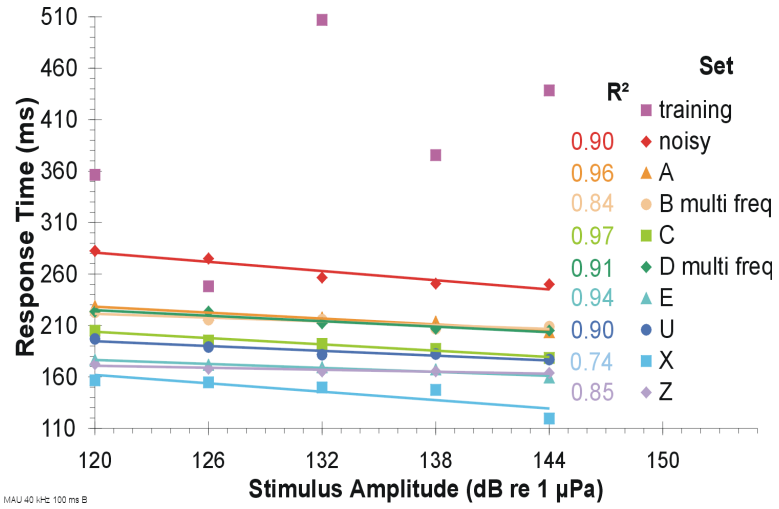

FIG. 11. Response times versus amplitude for MAU at 100 ms duration and 40 kHz frequency.

Carder, 1997) (Table II). Although there was only one data set with multiple amplitudes, response time showed an inverse relationship to stimulus amplitude at 100, 200 and 300ms (see Figure 13). Response times were slower when multiple frequency (100 ms duration) stimulus data sets were presented than when only one frequency was presented in a data set (Figure 14). Response times were generally slower with increasing stimuli duration (Figure 15).

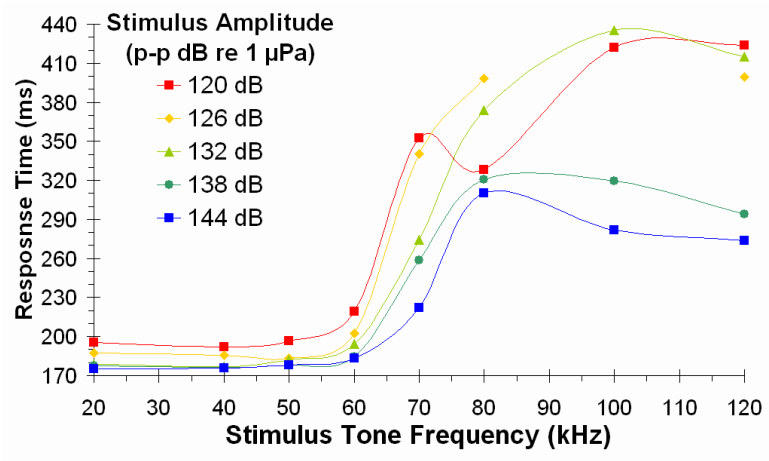

FIG. 12. Response times versus frequency for MAY for 100 ms duration for data set M.

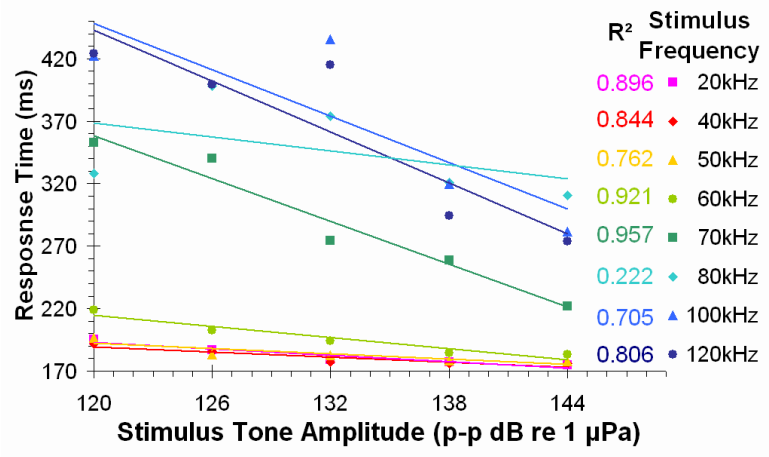

FIG. 13. Response times versus amplitude for MAY for 100 ms duration for data set M.

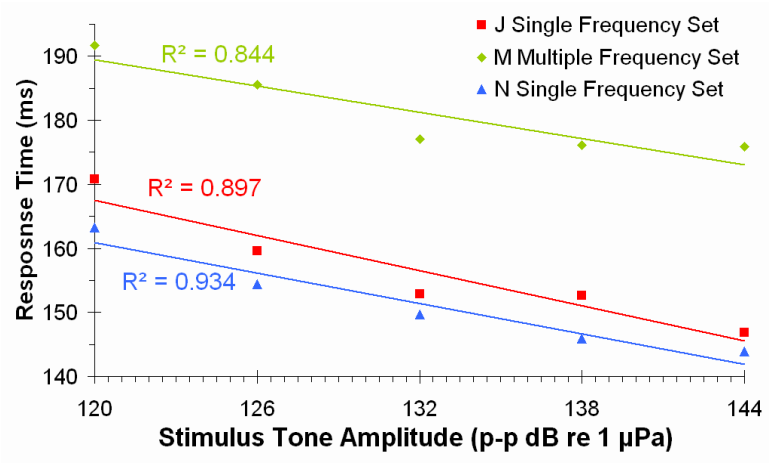

FIG. 14. Response times versus amplitude for MAY for 100 ms duration and 40 kHz frequency.

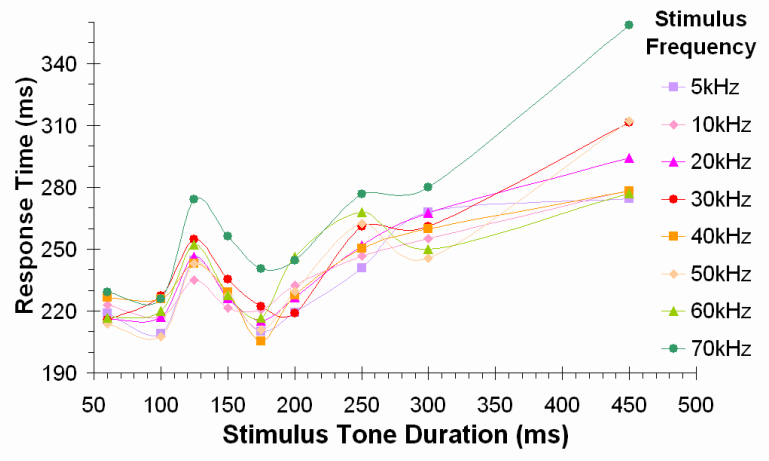

FIG. 15. Response times versus duration for MAY to 120 dB re 1 μPa stimulus tones.

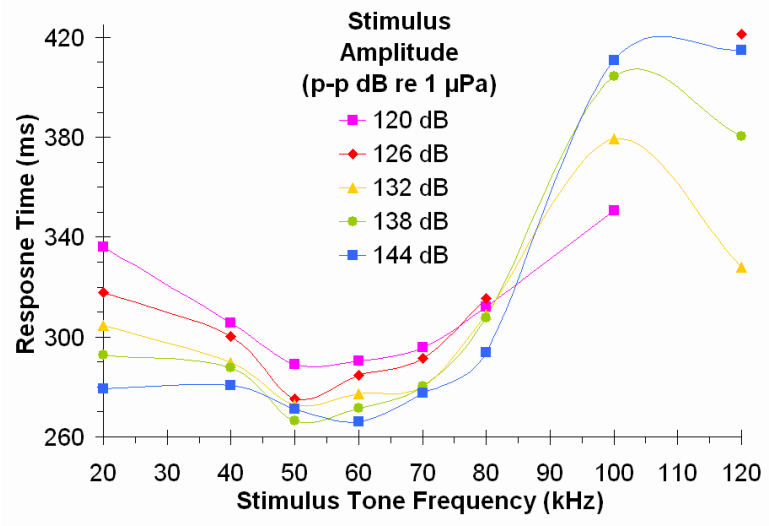

FIG. 16. Response times versus frequency for SLA for 100 ms duration for data set C.

The response time for SLA was more variable at 100 and 120 kHz (Figure 16). The rate of missed stimuli also increased at these frequencies (see Table II). Response time showed an inverse relationship to stimulus amplitude at 100 ms. Response times were slower when multiple frequencies of 100 ms duration tone stimuli were presented than when only one frequency was presented (Figure 17).

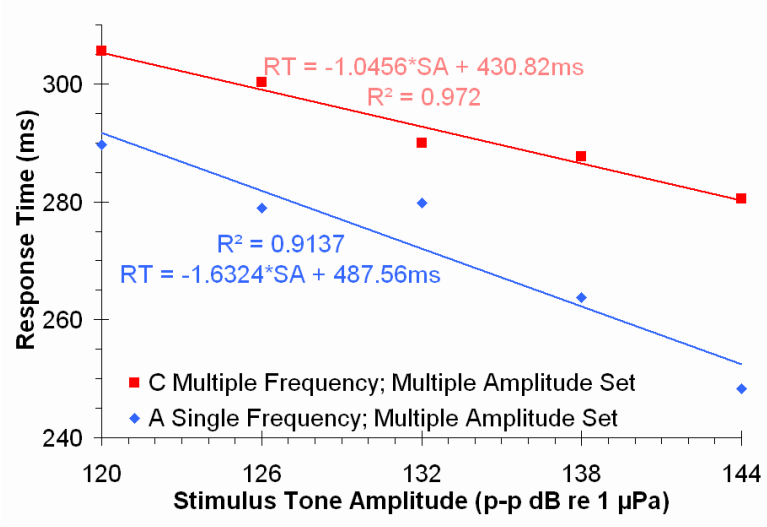

FIG. 17. Response times versus amplitude for SLA for 100 ms duration for 40 kHz frequency.

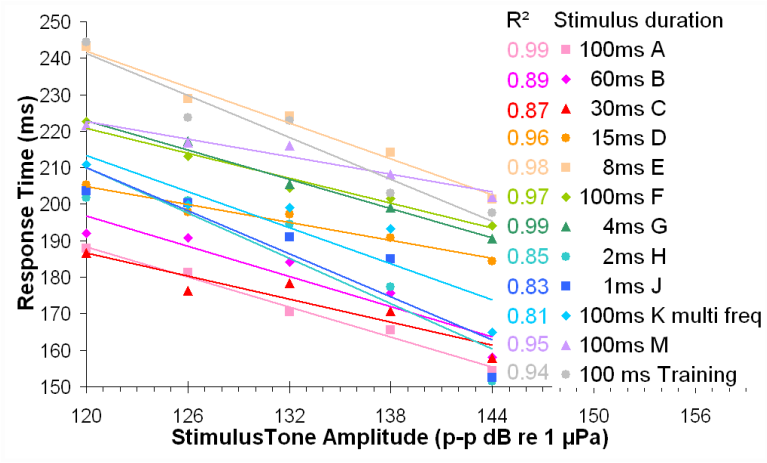

FIG. 18. Response times versus amplitude for TOD for 40 kHz frequency.

TOD participated in eleven data sets with multiple stimulus tone amplitudes where response time showed an inverse relationship to stimulus amplitude in most of these (Figure 18). Response time became slower in data sets going from 100 ms to 8 ms in temporal order presented (Figure 19). From 8 ms to 1 ms, the response time generally became faster. Response times in the 100 ms sets that were repeated generally became slower over the months. The effect of multiple frequencies within a data set on response time, at 100 ms and 40 kHz, are less clear for TOD (Figure 20). Response time was relatively flat across frequencies from 20 kHz to 120 kHz.

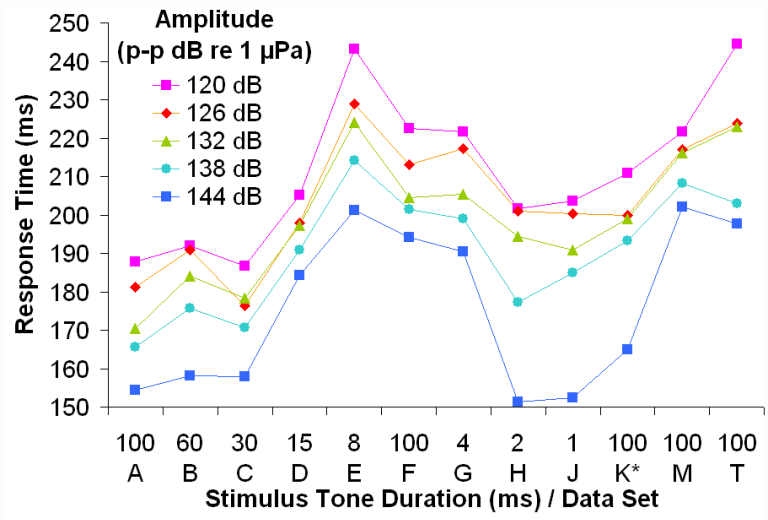

FIG. 19. Response times by data set for TOD. All stimuli were 40 kHz. The order of data sets on the X-axis is the order in which the experiments were performed.

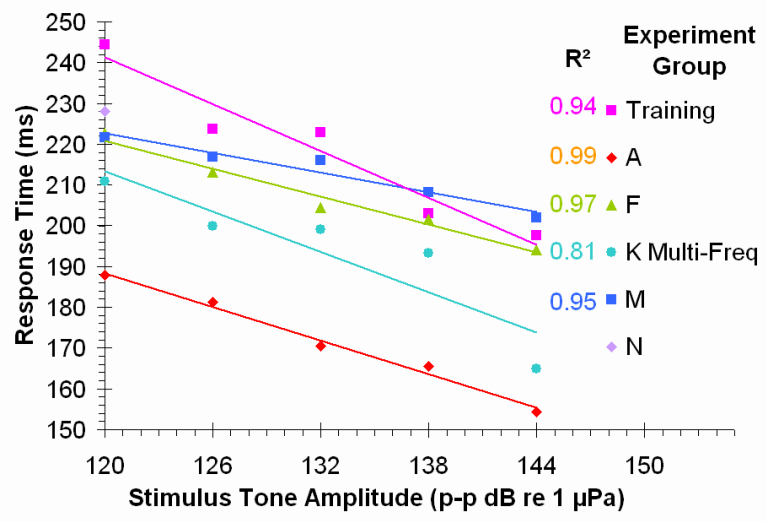

FIG. 20. Response times versus amplitude for TOD for 100 ms duration and 40 kHz frequency.

2. Effect of multiple frequencies in an experiment

In tests of the dolphins, some experiments tested a single frequency, while others presented stimuli at multiple frequencies in an experiment. The frequencies were presented randomly at intervals ranging from 1.1 to 2.1 s during a dive of 30 s to 2 minutes duration. In this section, I present comparative results concerning the effect of multiple frequencies on response times to 100 ms, 40 kHz, and 120 dB stimulus tones.

The subject APR participated in three studies. In studies A and C, all of the stimulus tones were at 100 ms, 40 kHz, and multiple amplitudes including 120, 126, 132, 138, and 144 dB. In data set B, the stimulus tones were at 100 ms, 40 kHz and multiple frequencies including 20, 40, 50, and 60 kHz. Testing of response times to 40 kHz, 100 ms, 120 dB stimulus tones across experiments with ANOVA found significant differences ($DF = 2$, $F = 3.827$, $p<0.03$). Testing for between-experiment differences with Fisher's PLSD found APR responded significantly faster in data set A (289.85 ms) than in data set C (326.83 ms), both of which were single frequency studies. Data set B (322.32 ms) was not significantly different from A or C ($p>0.07$ and $p>0.84$ respectively).

For subject MAU, the relevant response times are shown in Figure 21. Data sets A, C, and E all reflect single-frequency experiments at 40 kHz. Data sets B and D reflect multi-frequency experiments. Both B and D included stimuli at 20, 40, 50, 60, 70, 80, 100, and 120 kHz.

MAU participated in two multiple frequency data sets at 100 ms and nine other data sets at 40 kHz and 100ms. Testing of response times to 40 kHz, 100 ms, 120 dB stimulus tones across experiments with ANOVA found significant differences ($DF = 10$, $F = 77.14$, $p<0.0001$). MAU responded significantly faster in all but one (data

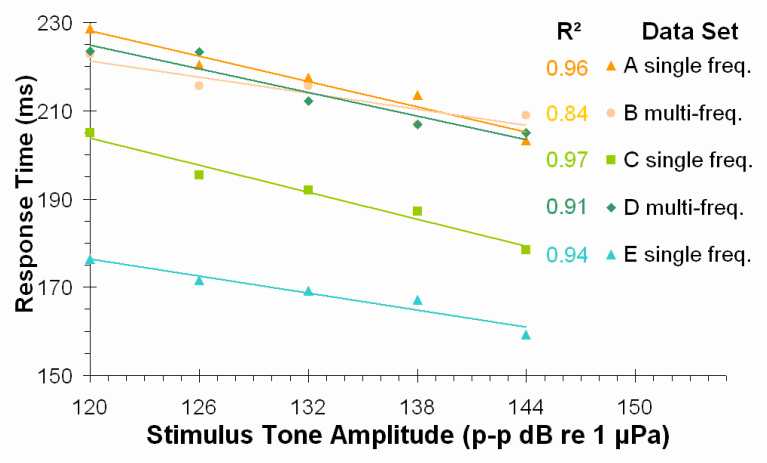

FIG. 21. Response times versus amplitude for MAU for 100 ms duration and 40 kHz frequency. Single frequency data sets at 40 kHz were compared to the 40 kHz data from multiple frequency data sets.

set A, $p>0.1$) of the single frequency data sets than in the multiple frequency data sets (all other $p<0.001$). Testing for between-experiment differences with Fisher's PLSD found that experiments B and D, the multiple-frequency experiments, were not significantly different ($p=0.8783$). MAU's first data set (A) had parameters of 40 kHz, 100 ms, and 120-144 dB. MAU responded slower to 40 kHz, 100 ms, and 120 dB stimuli in data set A than in any other data set.

For subject MAY, the relevant response times are shown in Figure 22. Data sets J and N reflect single-frequency experiments at 40 kHz. Data set M was a multi-frequency, multi-amplitude experiment. Data sets A, B, C and D reflect multi-frequency, single amplitude (120 dB) experiments. Data sets A, B, C and D included stimuli at 5, 10, 20, 30, 40, 50, 60, and 70 kHz. Data set M included stimuli at 20, 40, 50, 60, 70, 80, 100, and 120 kHz.

MAY participated in five multiple frequency data sets at 100 ms and two other data sets at 40 kHz and 100ms. Testing of response times to 40 kHz, 100 ms, 120

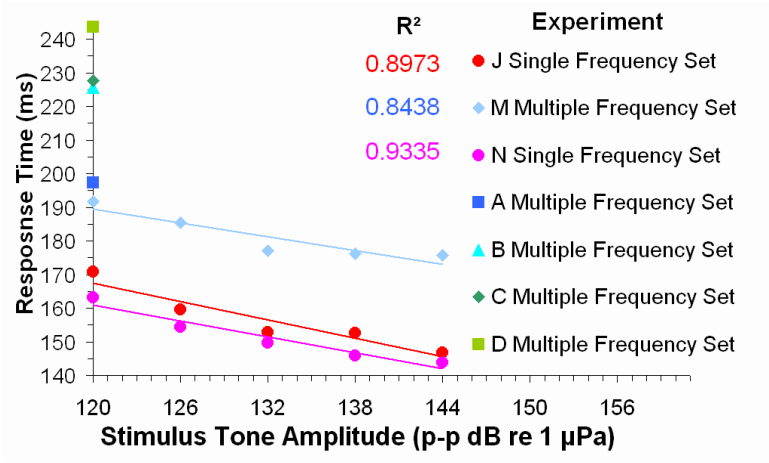

FIG. 22. Response times versus amplitude for MAY for 100 ms duration and 40 kHz frequency. Single frequency data sets at 40 kHz were compared to the 40 kHz data from multiple frequency data sets.

dB stimulus tones across experiments with ANOVA found significant differences (DF = 6, F = 46.30, $p<0.0001$). Testing for between-experiment differences with Fisher's PLSD found that MAY responded significantly faster in the single frequency data sets than in the multiple frequency data sets ($p<0.05$).

For subject SLA, the relevant response times are shown in Figure 17. Data set A reflects single-frequency experiments at 40 kHz. Data set B was a multi-frequency, single amplitude (120 dB) experiment and included stimuli at 5, 10, 20, 40, 60, 80, 100, and 120 kHz. Data set C was a multi-frequency, multi-amplitude experiment and included stimuli at 20, 40, 50, 60, 70, 80, 100, and 120 kHz.

Testing of response times to 40 kHz, 100 ms, 120 dB stimulus tones across experiments with ANOVA found significant differences (DF = 6, F = 46.30, $p<0.0001$). Testing for between-experiment differences with Fisher's PLSD found that for SLA each experiment was significantly different from the other two ($p<0.0005$). SLA responded quickest in the multiple frequency, single amplitude data set and slowest

in the multiple frequency, multiple amplitude data set.

For subject TOD, the relevant response times are shown in Figure 20. The training data set and data sets A, F and M reflect single-frequency experiments at 40 kHz. Data set K was a multi-frequency, multi-amplitude experiment and included stimuli at 20, 40, 50, 60, 70, 80, 100 and 120 kHz. Data set N was a multi-frequency, single amplitude experiment and included stimuli at 5, 10, 20, 40, 60, 80, 100 and 120 kHz.

Testing of response times to 40 kHz, 100 ms, 120 dB stimulus tones across experiments with ANOVA found significant differences ($DF = 5$, $F = 56.71$, $p<0.0001$). Testing for between-experiment differences with Fisher's PLSD found that TOD responded fastest in data set A ($p<0.0001$). She responded the second fastest in the multi-frequency data set (K). TOD was significantly faster in K than in M, N and T (training), but she was not significantly faster in K than in data set F.

3. Tests on whales

None of the data sets presented to MUK had multiple amplitudes. There was only one duration (300 ms) in which the relationship between stimulus amplitude and response time followed the expected pattern across all frequencies (Figure 23). In the six other durations presented to MUK there was no clear relationship between stimulus amplitude and response time.

NOC was available only for limited participation. NOC showed no clear pattern in the relationship between response time and frequency or duration. All but one data set presented stimuli at 120 dB. The only other amplitude presented was at 108 dB; therefore there were insufficient data for examining the relationship of response time to stimulus amplitude.

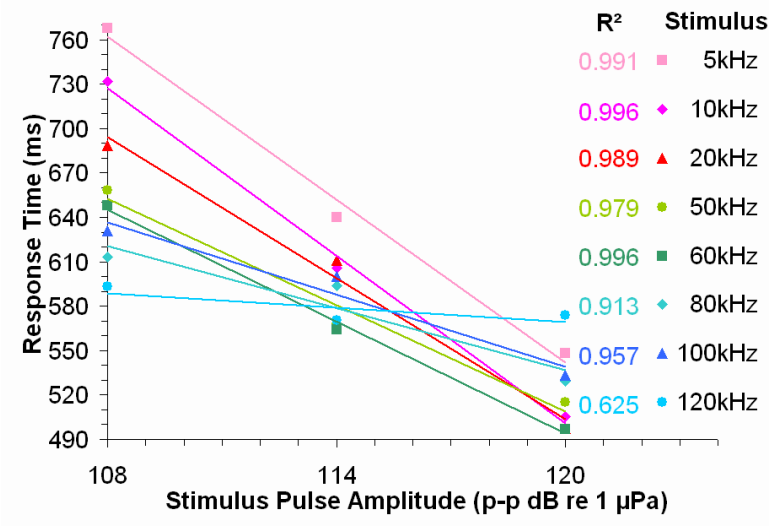

FIG. 23. Response times versus amplitude for MUK at 300 ms duration.

D. Discussion

1. Treatment of outliers

An extended discussion of the treatment of outliers was given by Ratcliff (1993). Outliers were defined by Ratcliff as "response times generated by processes that are not the ones being studied". There were, in effect, two types of outlier rejection utilized in the analysis done here. First, there was a hard limit imposed by the experimental procedure. The recording equipment saved only 1200 ms of data from the start of a stimulus. If the subject did not respond within that window of time, any response exceeding that limit was rejected. Second, responses falling outside of 2.0 standard deviations per subject per data set were rejected. Ratcliff's choices of rejection functions were 1.0 and 1.5 standard deviations. I selected a more conservative function for the data collected here as recommended in Weisbrot (1985).

2. Effect of task complexity

In choice reaction time, the subject responds slower as the number of equally probable alternatives increase (Hick, 1953; Hyman, 1953). I postulated that even in a simple reaction time task, response time would increase as the listening task became more complicated. The animal uses the same response to all tone stimuli regardless of tone frequency, duration or amplitude, but the search image, and thus listening task, is more complex in a session in which more than one frequency was presented.

Response times should be faster for single frequency data sets when looking at the same frequency and stimulus amplitude. For MAU, MAY and SLA the data support this (cf. Figures 21, 14, and 17). TOD's data are inconsistent with this hypothesis, as the response times for multi-frequency stimulus in general were faster than for single frequency stimuli (cf. Figure 20). APR's data neither supported nor contradicted the hypothesis that listening to multiple frequencies was a complex task.

3. Variation between subjects of the same species

There was a substantial amount of variation in the response times between individuals (cf. Figures 7 and 6). In general, the older dolphins (MAU, age 32, and TOD, age 32) responded faster than the younger dolphins (Figure 24). This finding may be attributable to practice and familiarity with test tasks.

A preliminary analysis of this simple reaction time data caused Ridgway and Carder (1997) to examine hearing loss in several of the subjects. The features that led to this suspicion were the longer response times and diminished percentages of correct responses noted for these subjects across a broad range of high-frequency stimuli (see Figures 9 and 12). This evaluation was performed in 1993, and it indicated that MAU, MAY and SLA had some high frequency hearing loss at and above 60 kHz,

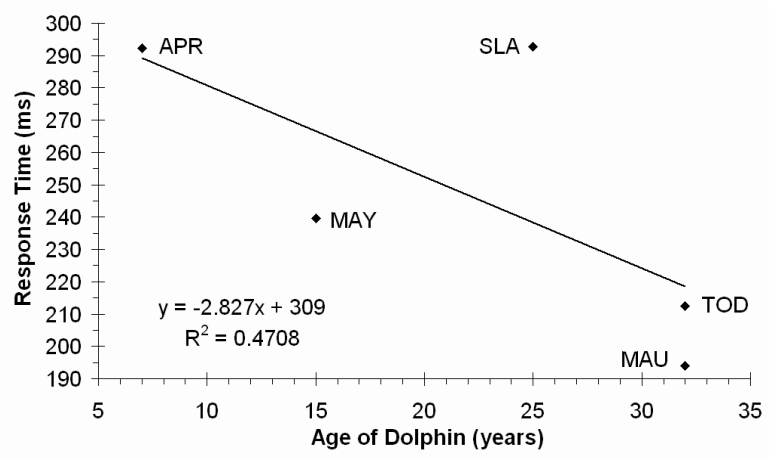

FIG. 24. Response times versus age of subjects.

80 kHz and 100 kHz, respectively. TOD was also tested in the study and showed no indication of hearing loss from 40 kHz through 120 kHz. The pattern of diminished correct responses and longer response times was also seen in testing response times in terrestrial mammals with hearing deficits (Ridgway and Carder, 1997).

4. Differences between species

While intra-species variation was substantial, between-species comparisons showed a significant difference in response times. The white whales were significantly slower. Because white whales are significantly larger than bottlenose dolphins, the question of allometric change as a factor is immediately raised. In Figure 25, a power curve was fitted to points defined by the weights and mean response times for all subjects. The points for the five dolphins fall in the lower left part of the plot, while the two white whales fall on the right. The resulting exponent of the fitted power curve was 0.45. A typical allometric relation from physiological studies might have an exponent of about 0.67. The R^2 value of 0.49 indicates that increasing weight can explain almost

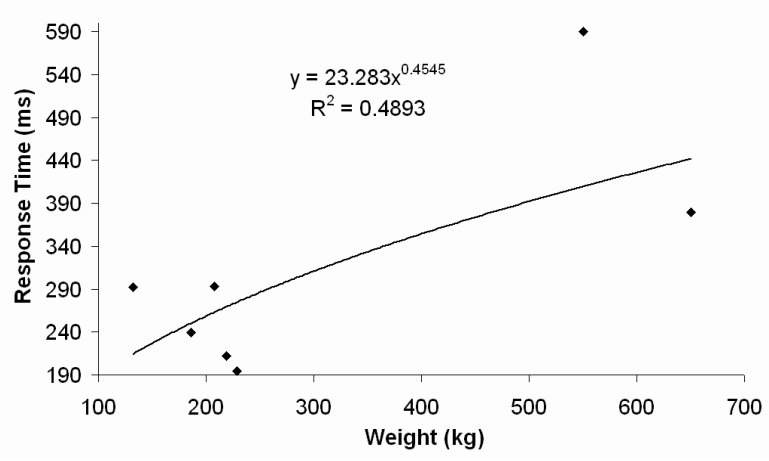

FIG. 25. Response times versus weight for all subjects for stimuli well above threshold.

half of the observed variation in response times.

The slower response times of white whales may be a constraint enforced by the physics of size and physiology. There is an interaction here between white whales as predators and their prey. Response times may play a role in choice of prey species, and thus have a shaping factor on the niche of white whales. Conversely, the faster response times of bottlenose dolphins may permit them to consistently succeed in taking prey items that might more frequently elude a white whale.

5. Similarities to terrestrial animals

Simple response time studies in both terrestrial animals and the species studied here show a decrease in response time with increasing stimulus amplitude (Wells, 1913). This broad relationship holds in all animal groups thus far examined.

Comparative studies of response times across species are rare. One factor that contributes to this is that, for an effective comparison, one must have the same experimental conditions hold across species. As noted earlier, studies have varied

on the parameters of stimuli presented, on the means by which subjects responded to stimuli, and environmental conditions during testing. It is not a simple matter to attempt to reconcile the differences in experimental conditions in order to review past work and obtain comparative results.

E. Conclusion

For this study on simple acoustic response times, white whales and bottlenose dolphins responded to higher amplitude stimuli faster than they responded to lower amplitude stimuli. This relationship between stimulus amplitude and response time is well known from previous work on terrestrial animals (Stebbins, 1966, 1970).

The average response time for bottlenose dolphins was 231.9 ms. The average response time for white whales was 584.1 ms. There was considerable variation between subjects within a species, but the difference between species was also found to be significant. White whales have longer response times, on the average, than bottlenose dolphins. The difference in size may explain much of this difference in response times.

Response time studies have the potential to reveal much about the cognitive processes of animals in a non-invasive manner. The most effective use of response times would be in comparative work that allows inferences to be drawn concerning evolutionary and ecological implications. Future work on simple response time should be conducted in such a way as to maximize the number of species to which the same experimental procedures can be applied. A commonality of experimental design across experimenters and subject species would maximize the utility of the resulting data.

CHAPTER III

SIMPLE RESPONSE TIME DURING A HEARING THRESHOLD TEST

A. Introduction

In general, simple response time has been found to decrease as intensity of the stimulus increases. This has been found in various stimulus modes including electrical (Cattell, 1886b,c), auditory (Stebbins and Miller, 1964; Stebbins, 1966; Green, 1975; Pfingst *et al.*, 1975a; Dooling *et al.*, 1978), and visual (Hick, 1953; Hyman, 1953). Researchers found little effect of the frequency of light on response time (Homes, 1926; Cattell, 1886b,c). Figure 26 shows typical relationships between response time and stimulus amplitude for several studies in humans.

Equal loudness curves plot the stimulus amplitudes needed for a subject to perceive the same loudness across different frequencies with a reference to 1 kHz. The loudness equivalent to a dB level at 1 kHz is termed a phon. So the loudness at 20 dB at 1 kHz is 20 phons and the amplitude needed for the subject to perceive the same loudness at another frequency is also 20 phons.

Equal latency curves plot the stimulus amplitudes needed to maintain a constant response time across different frequencies. When equal loudness and equal latency curves have been calculated for the same subject (Pfingst *et al.*, 1975a; Kohfeld *et al.*, 1981), they tend to create similar, but non-identical contours. Kohfeld found a greater change in response time from 20 to 40 phons at 1 kHz than at higher or lower frequencies. The relationship between phons and response time was more consistent (and more linear) at 60 and 80 phons.

When equal loudness curves have been calculated, they tend to follow the same general shape across frequencies as the audiogram for that species. Slower equal latency curves tend to be closer to the threshold and follow the audiogram shape

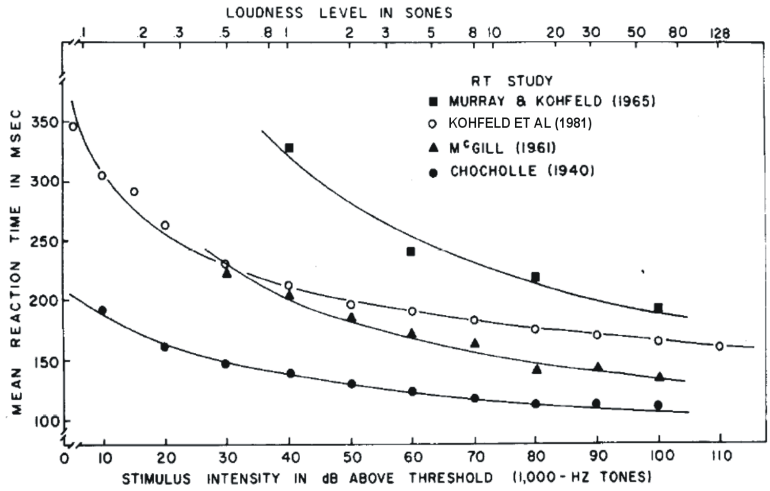

FIG. 26. The relationship between stimulus intensity and response time. Data points are means and for each study are as follows: (1) Murray & Kohfeld, 120 from 10 unpracticed subjects; (2) Kohfeld, 48 from one practiced subject; (3) McGill 20 from one "typical" practiced subject; and (4) Chocholle, at least 100 from one highly practiced subject. From Kohfeld *et al.* (1981).

more closely. Faster equal latency curves tend to be flatter as do equal loudness curves. Possibly perceived loudness rather than the frequency *per se* affects the response time.

As stimulus amplitudes are decreased from well above threshold to near threshold, response times have been shown to increase (see Figure 26). The slope of a line fitted through points taken in the same study is higher for the points near threshold than for the ones well above threshold. At stimulus amplitudes well above threshold, the relation between response time and amplitude in decibels is nearly linear. In chapter II, I examined data from a response time study with stimuli well above threshold. In this chapter, I present results from a study with data taken near threshold (Figure 4).

Tursiops truncatus has been the species most often trained for experiments and studied as representative of cetaceans. They have been successfully held in captivity since 1914. Bottlenose dolphins have a large auditory cortex and rely on hearing for communication and their use of biosonar. Their skill at biosonar intrigues people and stimulates interest in their auditory system. *Delphinapterus leucas* is one of the most vocal cetacean species, and have also been shown to be readily trained and adapt well in captivity.

A multi-year study of hearing in *Tursiops truncatus* and *Delphinapterus leucas* presented an opportunity to analyze a large data set of response times taken near threshold. Response times in this study were taken with varying stimulus amplitude, frequency, and masking noise levels. Based upon the results of previous response time work in other species, I expected response time to increase with an increased masking level and the same stimulus amplitude. I also expected response time to decrease as the stimulus amplitude increased.

B. Methods

The response time data analyzed here were collected during the baseline hearing tests as part of studies of masked temporary threshold shift in 1998 thru 2000. The methods for data collection of the basic hearing data were reported by Finneran *et al.* (2000); Schlundt *et al.* (2000); Finneran *et al.* (2002a,b), using the following description. The hearing tests were performed using the method of free response. A staircase method was used to determine threshold. Data were collected in San Diego Bay which has highly variable natural and man-made noise. Masking noise was generated to provide consistent background sound. In human studies, the presence of masking noise elevates thresholds and increases response time. Although the focus of the overall study was temporary threshold shift, this work examines response time in data where there was no hearing threshold shift observed due to prior high amplitude fatiguing stimuli.

Several separate experiments were conducted during the three year period (cf. Table III). This analysis focuses on response time during each of these.

1. Subjects

Four Atlantic bottlenose dolphins (*Tursiops truncatus*) and two white whales (*Delphinapterus leucas*) ranging in age from 16 to 35 years participated as subjects in this study (see Table IV). There was insufficient data from two of the *Tursiops truncatus*; therefore data from only two subjects of each species were analyzed. The animals were housed in wooden floating pens (10 x 10 m to 13 x 25 m) with netting to form an enclosure located in San Diego Bay, California. All animals were kept in accordance with applicable federal regulations under constant veterinary supervision. Diets included herring, mackerel, capelin, smelt and squid in specific amounts to

TABLE III. Description of equipment for behavioral audiogram experiments.

Project	S1 Equipment			S2 Equipment			
	Projector	Amplifier	Freq. (kHz)	Projector	Freq. 1 (kHz)	Freq. 2 (kHz)	Freq. 3 (kHz)
A	ITC1001	Hafler P7000	3	ITC1032	3	4.5	6
B	ITC2015	Instr Inc	3	ITC1032	3	.	.
C	ITC2015	Instr Inc	3	ITC1032	4.5	.	.
D	XF4 (8)	Instr Inc	0.4	ITC1032	0.6	.	.
E	ITC1001	BGW PS4BM	20	ITC1032	30	.	.
F	ITC1001	BGW PS4	10	ITC1032	25	30	35
G	ITC1001	BGW PS4	10	ITC1032	3	4	30
H	ITC1001	BGW PS4M	10	ITC1032	20	.	.
I	ITC1001	BGW PS4M	10	J13	0.4	4	.
J	ITC1001	BGW PS4	10	ITC1032 & USRD J13	0.4	4	30

TABLE IV. Summary data on subjects for behavioral audiogram experiments.

Code	Species	Gender	Weight (Kg)	Length (cm)	Age	Est. Birth Year
BEN	*T. truncatus*	M	270	270	35	1964
BUS	*T. truncatus*	M	190	247	18	1981
MUK	*D. leucas*	F	550	350	31	1968
NEM	*T. truncatus*	M	227	271	33	1966
NAY	*T. truncatus*	M	250	285	16	*1983
NOC	*D. leucas*	M	650	400	22	1977

* Born at the Navy Marine Mammal Program

maintain a healthy weight relative to the animal's age, size and gender. Performance and number of work sessions per day did not affect the amount of food the animal received. The study protocol was approved by the Institutional Animal Care and Use Committee under the guidelines of the Association for the Accreditation of Laboratory Animal Care (Finneran *et al.*, 2000). At the time of the study, the subjects were healthy and not known to have any hearing loss at any of the tested frequencies. One subject, MUK, did have an elevated hearing threshold at 40 kHz relative to 30 and 45 kHz prior to the start of this work (Ridgway *et al.*, 2001).

Tursiops truncatus (Johnson, 1967) and *Delphinapterus leucas* (White, Jr. *et al.*, 1978; Awbrey *et al.*, 1988; Johnson *et al.*, 1989; Ridgway *et al.*, 2001) have hearing ranges and sensitivities equivalent to or better than many marine mammals (Fay, 1988; Richardson *et al.*, 1995) based on behavioral audiograms (Figure 4). So, *Delphinapterus leucas* and *Tursiops truncatus* may be considered representative of

many marine mammals for both broad bandwidth and high sensitivity and may be impacted by a wide range of anthropogenic underwater sound. Both species belong to the superfamily Delphinoidea, which includes over half of all cetaceans (Ridgway, 1997).

2. Hearing test framework

The testing setup included a computer and equipment shelter and a 13 x 13 m test enclosure, similar to the housing enclosures, with two listening stations for the animals as shown in Figure 27. There were two underwater listening stations, labeled "S1" and "S2". Each station was built of polyvinyl chloride (PVC) frame with a plastic biteplate that the animal held during the hearing task, keeping the head stationary. The depth for S1 was 2.5 m for the data collected in 1998 and 4.27 m for data collected from 1999 through 2001. The S2 bite plate depth was 2.0 m. Both stations were equipped with an underwater sound projector (Figure 27, projectors A and D) and a receiving hydrophone (Figure 27, hydrophones B and C). Masking noise was presented at S2 with projector E (Figure 27). The masking noise projector (C) in Figure 27 was at the same depth as the biteplate and between 0.8 m and 2.1 m distant from the subject depending on the experiment. In 1998, the S2 hearing test projector was 1.5 m below the biteplate as part of data collection for work on the effect of projector position by Schlundt *et al.* (2003). From 1999 to 2001, the S2 projector was above the bite plate. These positions of projectors were recorded on datasheets for each day of data collection.

Underwater video cameras provided a top view of each of the stations. These were used to confirm that the animal was correctly positioned on station. The subject was asked to restation if not in the correct position. A third video camera recorded an in-air view of the test enclosure.

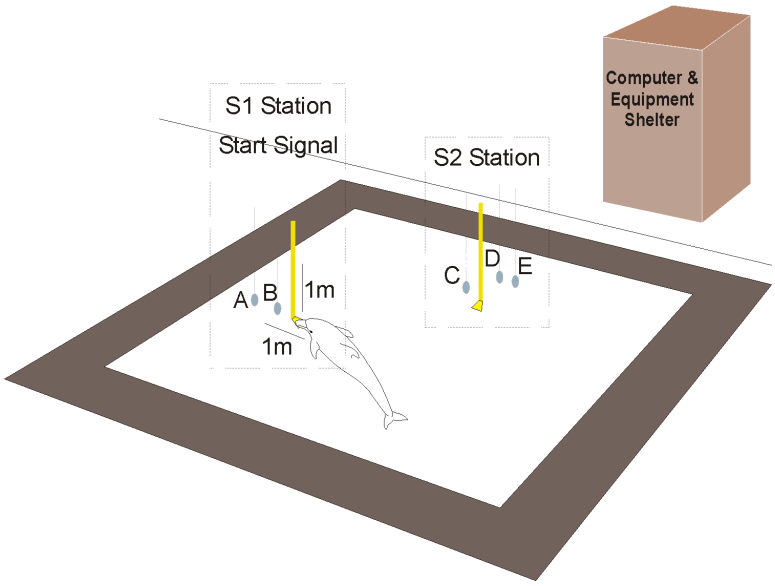

FIG. 27. Schematic of hearing test area and equipment.

3. Equipment

A suite of electronic equipment was needed to provide calibrated tones and recordings for the hearing tests.

The 1 s tones for the S1, or "go signal", were generated by a Wavetek 178 with the timing controlled and recorded by the control computer. The S1 tones had approximately 0.5 ms rise and fall times. The signal was filtered through an Ithaco 4302 and amplified by a Hafler P700C, Instruments, Inc or a BGW PS4 as needed. The signal was delivered to a projector suitable for the frequency required (cf. Table III). The power amplifiers used have total harmonic distortion figures of less than 0.035% and a slew rate of 40 volts/ms, thus not limiting the ramp-up rates of the tones. The S1 projector was directly in front of the subject at a distance of one to two m depending on the experiment. A Brüel & Kjäer 8105 was used to record the S1 signal.

The animals were trained to listen to a 1 s start tone signal (S1) at one listening station (S1 station). The end of the one second tone cued the animal to swim to a second listening station (S2 station) for the hearing test. The S1 signal was set at 141 dB re 1 μPa received *sound pressure level* (SPL) for 1998 and 1999; 141 dB was the median of the amplitude range of 103 to 179 dB previously recorded for dolphin whistles (Ridgway *et al.*, 1997). In 2000 and 2001, the S1 amplitude was set to 120 dB.

S2 tones were generated using a digital computer and multifunction board (National Instruments PCI-MIO-16-E1), filtered (Ithaco 4302 or 4212), and amplified (BGW PS2A) before being input to a projector appropriate for the frequency (see Table III).

The animals had been trained to respond by whistling when they heard a "hearing" test tone at the S2 listening station. Each hearing test tone was 0.25 s (250 ms) in duration. This duration was based on previous hearing studies of dolphins, in which reduction in stimulus duration increased thresholds (Johnson, 1968). The 0.25s duration corresponds to a short duration that is not expected to increase the hearing threshold of the subject. An HP 350B Attenuator was used as needed.

S2 signals and any animal vocalizations were monitored with a Brüel & Kjäer hydrophone attached to the S2 station between the animal and the projector. In order to record the same sound level as that received by the subject, the listening hydrophone was placed next to the animal's jaw. Brüel & Kjäer 8103 hydrophones were good measurement hydrophones because of their consistent calibration response over a wide range of frequencies. Their calibration standards can be traced to the National Institute of Standards and Technology.

The recording equipment changed as equipment improvements were made. All measurement hydrophones were individually calibrated. The signal from the Brüel

& Kjäer 8103 was amplified by a Brüel & Kjäer 2635 charge amplifier set to the sensitivity of the hydrophone and adjusted during calibration with the Brüel & Kjäer 4223 calibrator (accurate to ±0.3 dB) and the HP 3561A analyzer (accurate to ±0.25 dB). The S2 receive hydrophone was a Brüel & Kjäer 8105 or the equivalent Reson model.

The computer control program generated files for the S2 presentations based on a table of parameters for control of the projection hydrophone. The signals were shaped to provide a 5 ms rise time of the tone to the full amplitude. D/A conversion was through a National Instruments PCI-MIO-16E-1 card. The output was amplified with a Hewlett-Packard HP 467A power amplifier and delivered via an ITC 1032 or J13 projector. The received sound pressure levels (SPL) of the projected tones were measured with the calibrated Brüel & Kjäer 8103 hydrophones. The repeated calibrations and measurements on the S1 and S2 monitor hydrophones kept the system accuracy within ±1 dB for all transmissions.

A two-line, 32 alphanumeric character, serial interface liquid crystal display was employed to present status information to the trainers remotely. It was used to present information such as the length of the current dive, the number of stimuli presented in the dive and session, the amplitude of the last stimulus, and whether a hit or a miss was recorded for the last stimulus presented.

4. Masking noise

Masking noise was used in these hearing tests because a low-noise test environment was not available. The noise in the bay was monitored through the S2 listening hydrophone as shown in Figure 27. When the noise level in the bay exceeded the masking noise, testing was stopped until the ambient noise fell below the masking noise. For 3 kHz testing, tug boats exceeded the noise level when they were in the

area, and testing was stopped. For testing in the 20 to 40 kHz range, it was necessary to increase the level of masking noise because of other noise present in that frequency range, especially from dolphins in nearby enclosures. The Gaussian masking noise was generated with a custom built noise generator, and a Wavetek 132 amplified with an HP 467A (1998). In 2000, custom software was created to generate Gaussian masking noise on a PC. D/A conversion was through a National Instruments PCI-MIO-16E-1 card. The output was amplified with a Hewlett-Packard 350B or 355D power amplifier, filtered with an Ithaco 4302 and a Stanford Research Systems 560 low-noise pre-amplifier and a Kenwood equalizer. The output was projected via an appropriate hydrophone (cf. Table V). A Hanning analysis window was used.

5. Training

The subjects were trained by operant conditioning techniques to respond to tones projected underwater via a hydrophone. They were rewarded for faster responses to encourage them to respond as quickly as possible. They were trained to station on a bite plate (that is, to bite a mouth piece) to maintain the position of the ears relative to the projecting hydrophone. They listened and responded to tone stimuli until given a conditioned reinforcer (sound with a 8 to 16 kHz up-sweep) followed by fish from the trainer. Early in training the subjects were reinforced for each correct response to a tone. Later, the subjects responded to a series of from one to forty tones. Periods of no-stimuli (quiet) were also presented, and an animal was reinforced for correctly remaining quiet during these "catch trials".

6. Procedure

The Method of Free Response (MFR) (Egan *et al.*, 1961) was used to test hearing. In this method, a subject is presented with a series of brief tones with the time interval

TABLE V. Summary of equipment used for production of masking noise during behavioral hearing tests. Subject abbreviations: B = BEN, M = MUK, N = NEM, C = NOC.

Date	Project	Subjects	Projector	Binwidth (Hz)	Noise BW low freq. (kHz)	Noise BW high freq. (kHz)
1998/03	A	B M N C	ITC 1032	37.5	1	10
1998/05	B	B M N C	nr	.	.	.
1998/05	C	B M N C	ITC 1032	37.5	0	10
1998/06	D	B M N C	Brown Sphere	3.75	0	1
1999/08	E	B M N	ITC 1032	.	7.5	52.5
2000/02	F	B	ITC 1032	.	15	45
2000/02	G	B M	ITC 1032	.	.	.
2000/02	H	B M	ITC 1032	.	5	35
2000/02	I	B M	ITC 1032		0.2	0.6
			or J9	.	2	6
2000/03	J	B M N	ITC 1032	.	0.2	0.6
to			and		2	6
2001/01			USRD J9		15	45

between tones pseudo-randomized. The listener does not know the time of the of the next tone. The listener responds when a tone is heard and should do nothing otherwise. In this study, the response was a whistle (Ridgway and Carder, 1997). In most studies of terrestrial animals, the response was some form of key press or key release. A staircase procedure adjusting the amplitude level was used until threshold was determined. In this staircase method, the amplitude of the hearing tone was decreased by 4 dB each time the animal responded correctly. Each time the animal did not respond to a hearing test tone, the amplitude of the hearing test tone was increased by 2 dB. The animal was given two seconds to respond to a test tone. A response whistle given outside the two second whistle following a test tone was considered a false positive.

A dive or trial block began with the animal in front of the trainer and ended when the dolphin came up for air after responding to a series of test tones (see Figure 5). The animal swam to the S1 station after seeing the trainer's hand signal. The animal remained holding the bite plate until it heard the S1 tone, which was 1 s long and 141 dB re 1 μPa SPL at one m during baseline testing. The end of the S1 tone acted as the cue for the animal to swim to the S2 station bite-plate. Hearing test tones were delivered at randomized intervals from 5 to 10 s for up to 30 test tones for the dolphins and up to 40 test tones for the whales. The trainer used a projecting transducer to deliver a conditioned reinforcing signal at the end of a dive. This "bridge" or conditioned reinforcer was used to indicate that the subject had done well and fish would be given as a reward. The trainers used the trainer display to select when to bridge the subject. The bridge was typically given for the correct response to one of the lower amplitude tones or to a particularly fast response.

A hearing test consisted of sufficient trials to determine a hearing threshold and consisted of one or more dives. Each hearing test was saved in digitized form on the computer hard disk in a different event file.

7. Session

A session started when the animal was brought into the testing enclosure and consisted of one or more hearing tests. The session ended when the animal was sent out of the testing enclosure. Occasionally, due to bay noise or other delay, there was a longer waiting period between dives. Normally, the waiting period between dives was determined by the trainer, allowing the animal to rest and refresh its respiratory gas balance. Rarely, the animal spent the time between sessions in the testing enclosure if no other animal was being tested during the break between sessions. One to five hearing tests were done per session, with up to three frequencies tested per session. It took approximately one month to obtain stable noise limited hearing thresholds at each of the frequencies. Between one and four sessions were done on work-days with each session consisting of one or more hearing tests.

Hearing tests were in the following categories: baseline, pre-exposure (to a high amplitude sound), and recovery. Baseline sessions were done to establish consistent thresholds prior to exposure to a high amplitude sound and when the appropriate masking level was selected for each frequency. The latter three testing types were conducted as part of the Masked Temporary Threshold Shift (MTTS) testing and took place within one day. Pre-exposure was immediately prior to exposure to the fatiguing stimuli. Post-exposure was immediately after exposure. Recovery sessions were one to five hours post exposure to the fatiguing stimuli on the same day. For response time analysis, baseline and pre-exposure were considered to be the same type of session. Post-exposure and recovery data were also included when no MTTS

was observed.

When more than one frequency was tested per day, the order in which the frequencies were tested varied. Over the course of the experiment, the relative proportion of times a particular frequency was given in a particular place in the order between days was made approximately equal, or *counter-balanced*.

8. Threshold estimation

The mean SPL of the first ten hit-miss or miss-hit reversal points within the staircase data defined the subject's threshold for that data hearing test. Threshold estimation typically took from one to four dives or from 20 to 30 test tones (Figure 5). The threshold determination described here attempts to estimate the SPL at which the subject would respond to 50% of the trials.

9. Software

The S1 and S2 signal outputs, animal responses, and ambient noise were recorded by a control computer. A set of programs written in Borland's Delphi and National Instruments Labview were custom written for calibration, data collection and data analysis.

The data collection program utilized a response recognition routine to determine if the animal responded to a tone and when the response started.

10. Auto-detection routine

Prior to the development of the auto-detection routine, the operator classified each response manually at the time it was made in order to get correct staircase operation.

An improved auto-detection routine was built by implementing several detection methods and evaluating each in terms of success of detection, avoidance of false

positives and computational time. Each method had parameters that were used to customize the method for individual animals.

The auto-detect routine, like the data collection program, was implemented in Borland's "Delphi" development environment. This is a variant of the Pascal language with additions made for object-oriented programming and access to Windows primitives. The Delphi compiler produces well-optimized code, and has several useful debugging features. The auto-detection routine, or "Hound" unit, was 815 lines of code long, and established a "hound" object and its associated methods. Use of the unit in another Delphi program was accomplished by adding the name of the unit to the "uses" clause and declaring and initializing an instance of the hound object. An invocation of the hound method caused the auto-detection routine to be run. (See Figure 28.)

Variables were initialized and detection parameters assigned values based on the identity of the test subject. A reduced data representation of the acoustic data was used, in which the maximum value within a 1 ms time period is found. Other information related to the stimulus is also recorded within the record. This reduced data representation was called a "pix" record. Because the reduced data representation did not preserve full-bandwidth sampling, no spectral analysis was possible using a pix record. Instead, the amplitude and shape features are relied upon to determine whether or not a response is present within the sampled period.

In the first loop, several descriptors about the total pix record were calculated including the maximum, minimum, second maximum (second highest value) and second minimum (second lowest value). In addition, two histograms were determined, one for the time period of the test tone and the other for the rest of the data file. The histograms were used to determine the base levels of pix values when no response was present. Determination of these base levels was needed because some files have a

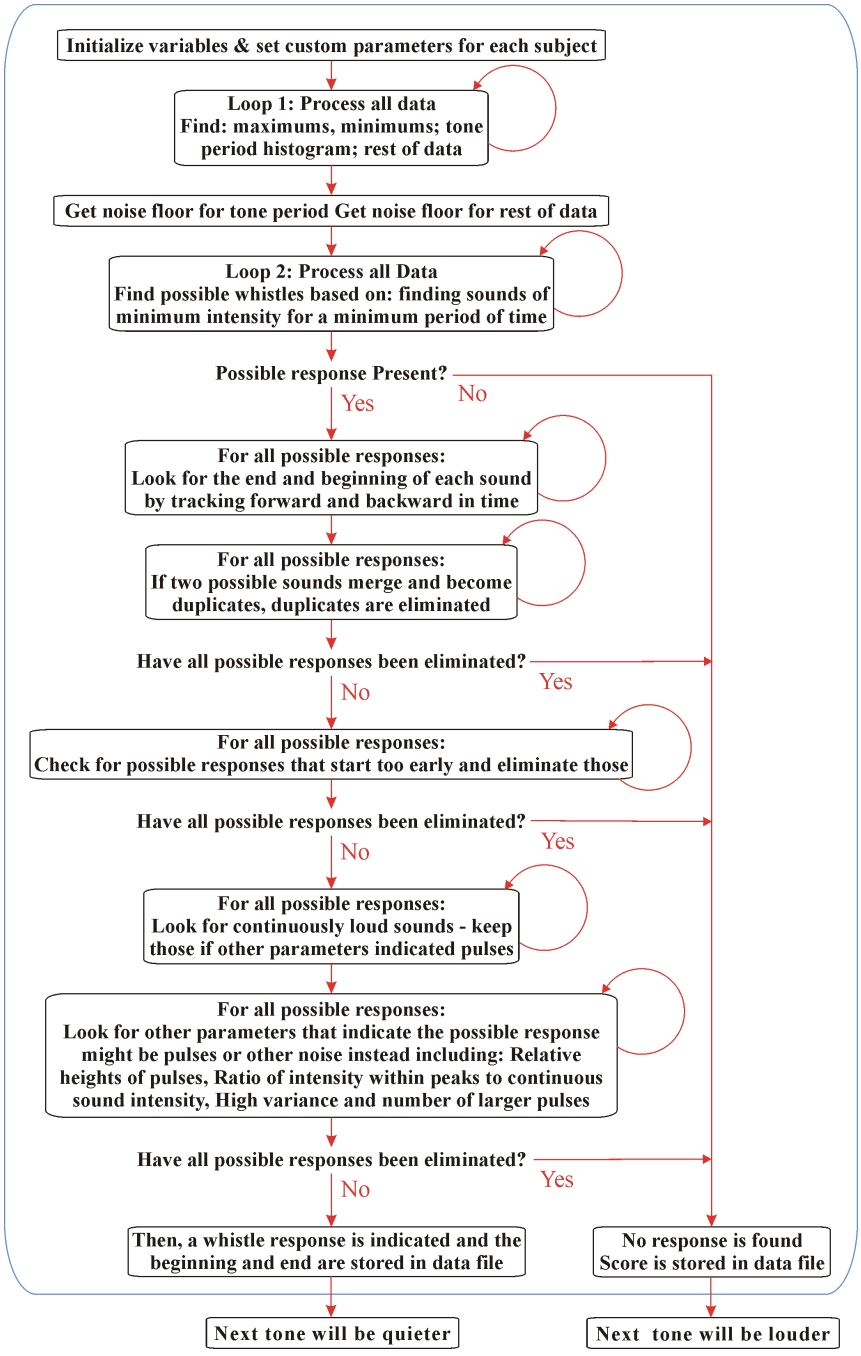

FIG. 28. Flowchart for the Hound algorithm.

DC offset. Two base values were needed because some of the higher amplitude tones created a detectable DC level during the test tone. The level of the test tone was needed to detect the beginning of responses that start during high amplitude tones. These early responses were seen primarily with the test subject BEN. To avoid setting a high base level for responses that started too early (and thus were false responses by the animal) further testing was done to look for a level DC offset rather than a variable amplitude sound. If a variable amplitude sound was found, it was not due to the contribution of the test tone, and the baseline for the time of the test tone was set to the same value as the baseline for the rest of the record.

The next loop looked for possible whistle responses by looking for sets of data points with a minimum value and of a minimum period of time at that amplitude above the base level. Then, each possible response was tested for being too early to be a valid response and was eliminated if it is too early. Next, the start and end of each possible response was determined by examining amplitude levels forward and back in time. Duplicate responses were eliminated. Then adjacent responses were merged if they were continuous in time. The process of eliminating any whistles that started too early (i.e., that were too short to account for normal brain response in mammals) was repeated if the start time was earlier after the search for the beginning of the whistle.

The rest of the routine looked at ways to eliminate possible responses whistles using a variety of parameters and calculations. The primary difficulty was rapid burst pulses. The pulses were so close together in time that they appeared to merge into a continuous sound. Continuously loud sounds were kept as they were unlikely to be burst pulses.

An important consideration was the discrimination of whistle responses from burst pulse responses. A check was done for very high amplitude continuous responses.

A response meeting this criteria was kept even if other parameters indicate the presence of pulses. Variance, the relative height of pulses, the number of larger pulses, and the ratio of amplitude within peaks to continuous sound amplitude were all used to discriminate rapid burst pulses from whistles.

The resulting determination of a whistle response and the time of the start of the response was returned to the main TTS program.

Testing of this routine was accomplished by analysis of historical data from audiometric tests of the marine mammals. The format of this data was a reduced representation, in which the maximum data values from each millisecond of acoustic data were stored. Whistles were scored as responses, and other vocalizations were rejected as non-responses. Over 48,000 separate response records from seven different subjects were analyzed and compared to hand-scored data, yielding an overall accuracy of 98.3% as shown in Figure 29. The program was developed using data collected in 1998. The routine was tested on novel data (data which had not been used for development) from January 1999. Comparison of performance showed similar results (Figure 30). The improvement in performance on NOC was due to training of NOC to respond with a higher amplitude whistle rather than improvement in the Hound algorithm. There were about twice as many false negatives as false positives. Several animals had low amplitude responses that were difficult to distinguish from background noise. Parameter tuning to achieve the lowest overall error rate resulted in missing those low amplitude responses.

An easy-to-identify response from NEM was shown on the user interface screen for the off-line test program (Figure 31). NOC's responses were of low amplitude and tended to be buried in the background noise (Figure 32). This led to the auto-detect routine missing detection of some responses, especially when there were burst pulses from other animals in the area (Figure 33). There were also some cases where

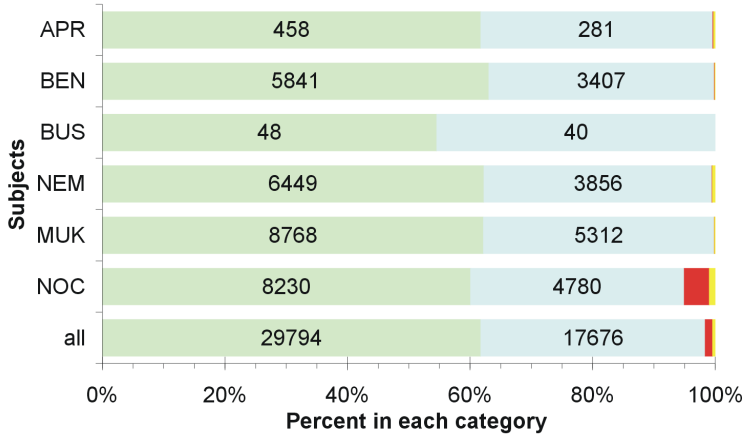

FIG. 29. Comparison of human and auto-detection algorithm in scoring data from 1998. Light green indicates agreement between algorithm and human on a response. Light blue indicates agreement between algorithm and human that there was no response. Red indicates that the algorithm scored no response, and the human scored a response. Yellow indicates that the algorithm scored a response, and the human scored no response. Note that in about three fifths of the trials the subject responded.

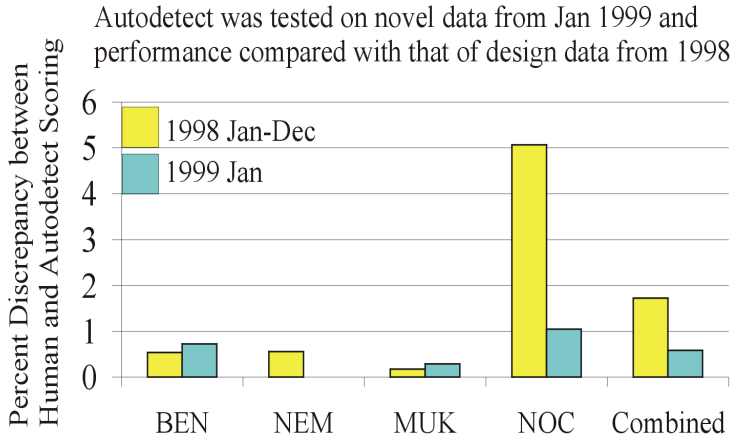

FIG. 30. Comparison of the performance of the auto-detection algorithm on development data from 1998 and novel data from January 1999.

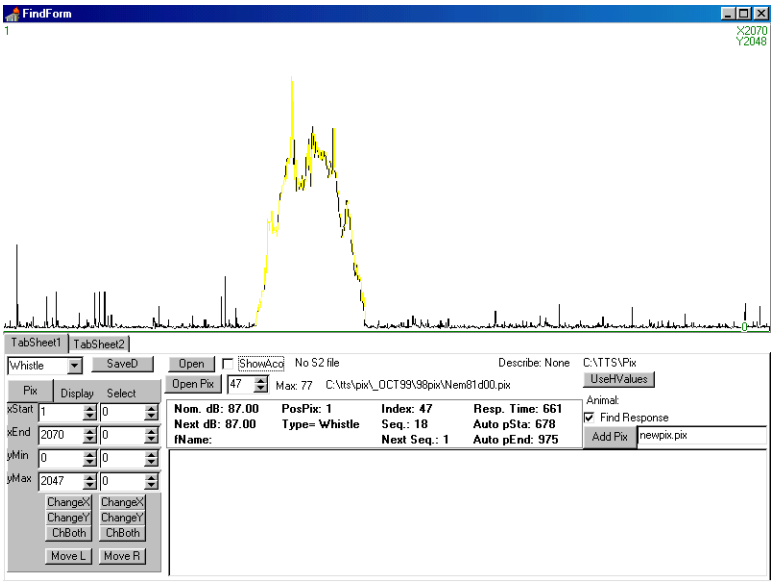

FIG. 31. User interface screen of test program showing a correctly scored whistle response for NEM.

FIG. 32. Auto-detect routine correctly found a low amplitude response from NOC. Responses with the similar energy as the noise floor were difficult to detect.

the Hound program incorrectly coded part of a burst pulse as a response (Figure 34). Some stimuli were of high enough amplitude to be visible on the display. Code taking high amplitude stimuli into account allowed the Hound to correctly indicate a finding of "no response" even with a high amplitude stimulus (Figure 35). The Hound program could still identify a response after a high amplitude tone (Figure 36). The Hound program correctly found "no response" even with a large burst pulse (Figure 37).

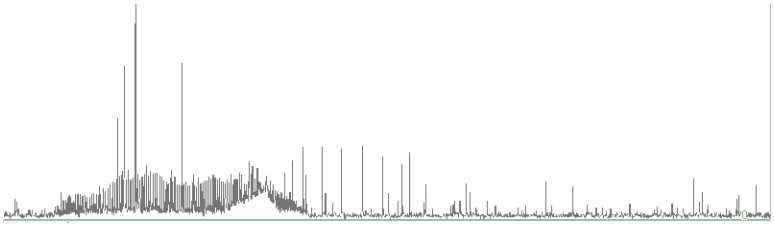

FIG. 33. Auto-detect incorrectly missed response buried in pulses from NOC. The pulse characteristics were identified and triggered rejection of a potential response whistle.

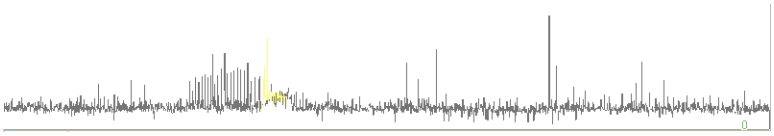

FIG. 34. Auto-detect routine incorrectly scored part of a burst pulse as a response from NOC.

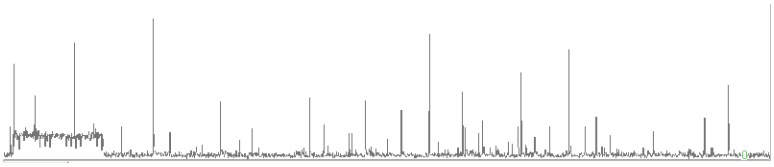

FIG. 35. Auto-detect routine correctly found "no-response" with a high amplitude, visible, stimulus from BEN.

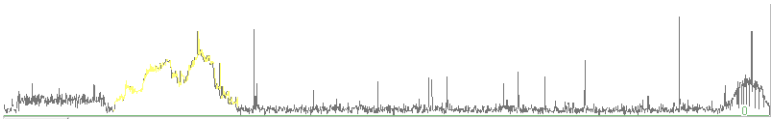

FIG. 36. Auto-detect routine correctly scored a response after a high amplitude, visible, stimulus from BEN.

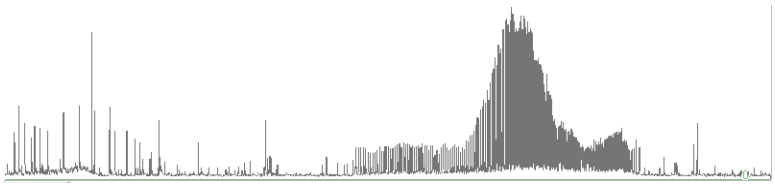

FIG. 37. Auto-detect routine correctly scored a "no response" in spite of a large burst pulse from NEM.

The amount of processor time taken by the auto-detect routine depends upon both the processor speed and the characteristics of the input data. An average time across all 1998 test tone data on a 90 MHz Pentium system was about 1.5 ms per invocation. Pix records with many excursions or possible responses took longer to process than pix records with just background noise recorded. The computational load imposed by use of the auto-detect routine for response detection was minimal.

Consistent detection of all responses has reduced the number of tones presented above threshold and allowed quicker reversals using the staircase method of threshold detection. Consistent avoidance of false positives has reduced the number of tones presented below threshold and again allowed for quicker reversals.

An automated response detection system excludes unconscious observer bias, eliminating this subjective factor. The auto-detect routine was also faster than the human observer and gave more rapid feedback to the trainers. This allowed the trainers to select the time to bridge the animals more accurately.

Auto-detection allowed the automatic recognition of false positive responses during zero-amplitude catch trials. This becomes important for calculations of *receiver operating characteristic* (ROC) curves as a measure of receiver bias in responses.

By having a reliable auto-detection algorithm determine presence of the response and time to response, more consistent response times were calculated. This aided in determining the difficulty of tone detection in near-threshold tones.

Prior to the development of the auto-detect algorithm, a person needed to hand-edit files to determine response time and presence of response. This was very time consuming and as a repetitive, tedious task could be better accomplished by a computer algorithm with the human simply reviewing the work for accuracy. The auto-detect routine scored the files, and the operator conducted a quick accuracy review.

11. Analysis

For analysis purposes, the hearing tests were divided into categories based on subject, frequency, and masking noise. Data from dives was discarded if extraordinary events occurred such as: human divers near the pen, pile driving, loose animals outside the work pen, loud noise from passing ships, tugs, or other sound sources. Means and standard deviations were calculated for each data set with the same combination of subject, frequency, masking noise, and stimulus amplitude. Data points outside of the mean plus or minus two standard deviations were discarded as outliers (Weisbrot, 1985). Linear regressions of the effect of stimulus amplitude on response time were calculated for each data set and tested for significance.

Response times were compared between species using a t-test. Response times were compared between individuals of the same species using analysis of variance. Least squares linear regression was calculated to examine the relationship between test tone amplitude and response time.

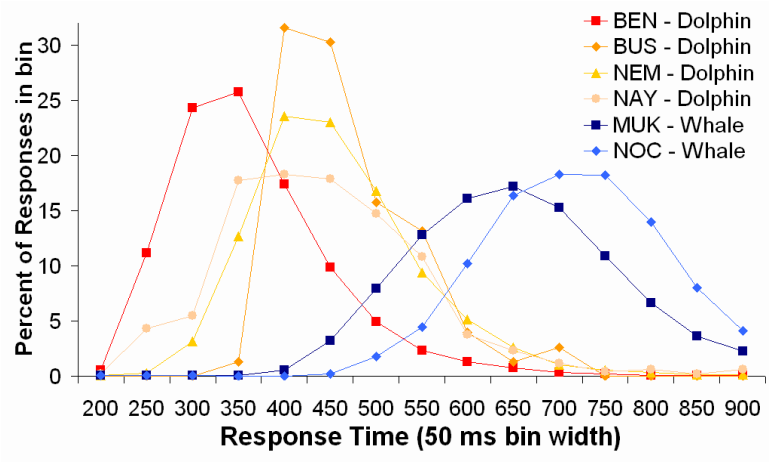

FIG. 38. Frequency polygon showing the distribution of response times for each subject over all stimulus frequencies and amplitudes at all masking levels.

C. Results

During the three years of the study there were over 60,000 responses used for response time analysis. Figure 38 shows frequency polygons of response times for all frequencies, masking noise levels, and stimulus amplitudes.

Responses from all frequencies, masking levels, and stimulus amplitudes were compared across subjects in an ANOVA on the basis of response time, length of response, amplitude of response, and estimate of energy of the response.

Analysis of response time via ANOVA split by subjects showed significant differences at $p<0.0001$ (5 DF, $F = 1669.445$) as is shown in Table VI. Using Fisher's *protected least significant differences* (PLSD) statistic, most between-subject comparisons were significant at $p<0.0001$. The response time for BUS was not significantly different from that of NEM or NAY. However, NEM was significantly slower than NAY at $p=0.0303$. Comparison of response time by species using a *t*-test found that the dolphins (414 ms) were significantly faster than the whales (672 ms) at $p<0.0001$

TABLE VI. Mean response characteristics by subject and species. Response amplitude is in relative units.

Subject	Time (ms)		Length (ms)		Amplitude	
	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.
Dolphins	414.1	144.964	378.1	137.026	403.0	265.26
BEN	372.6	134.217	409.1	143.976	414.3	252.601
BUS	468.2	72.625	675.1	81.48	466.0	152.741
NAY	453.4	135.633	580.6	311.657	322.0	232.591
NEM	466.6	141.752	325.5	76.738	391.7	281.969
Whales	672.3	133.724	201.6	56.343	499.2	425.076
MUK	661.4	133.458	211.7	54.013	574.0	426.985
NOC	725.9	121.537	152.5	39.115	132.5	104.019

(t = -214.373).

Analysis of length of response whistle via ANOVA split by subjects showed significant differences at $p<0.0001$ (5 DF, F = 11217.72) as is shown in Table VI. Using Fisher's PLSD, all between-subject comparisons were significant at $p<0.0001$. Comparison of length of response whistle by species using a t-test found that the dolphins' whistles were longer (378 ms) than the whales' (201 ms) at $p<0.0001$ (t = 199.114).

Analysis of relative amplitude of response whistle via ANOVA split by subjects showed significant differences at $p<0.0001$ (5 DF, F = 1594.666) as is shown in Table VI. Using Fisher's PLSD, most between-subject comparisons were significant at $p<0.0001$. The relative amplitude of response whistle for BUS was not significantly

different from that of any of the other animals. There were only 76 data points for BUS, while there were between 500 and 23,000 data points for all other animals. The whales represented the extremes, with NOC as the quietest animal and MUK as the loudest.

There were 91 data sets in this study with unique combinations of subject, stimulus frequency, and masking noise level. Of these, 52 data sets had a significant non-zero slope found by linear regression. Of the data sets with non-significant slopes, only four had more than 10 trials per stimulus amplitude.

1. Within frequency level

Response times at 3, 4.5, and 6 kHz, with masking near 63 dB compared to no masking in San Diego Bay, were approximately the same. Masking at 87 dB and 90 dB resulted in both a threshold shift and response time shift. See Figure 39 for an example.

Some data sets showed a marked increase in response time at threshold, as seen at 4.5 kHz with 87 and 90 dB masking noise levels (Figure 39).

At 400 Hz and 30 kHz, the relationship between response time and stimulus amplitude was similar at all masking levels tested for BEN.

Response times at 4.5 and 6 kHz, for masking near 63 dB and no masking in the San Diego Bay, were approximately the same. Masking at 87 dB resulted in both a threshold shift and response time shift.

Data for NEM at 30 kHz (Figure 40) showed that training resulted in responses to lower amplitude stimuli.

At 400 Hz, MUK's mean thresholds for 0, 85, and 95 dB masking levels were 108, 114, and 117 dB respectively. The mean response times increased with increasing masking level. At 6 kHz, MUK had almost the same response/stimulus amplitude

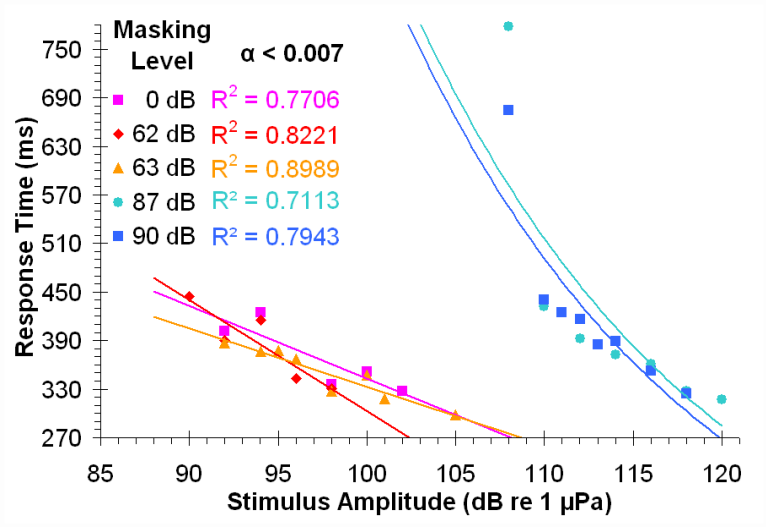

FIG. 39. Response time graph for BEN to 4.5 kHz stimuli.

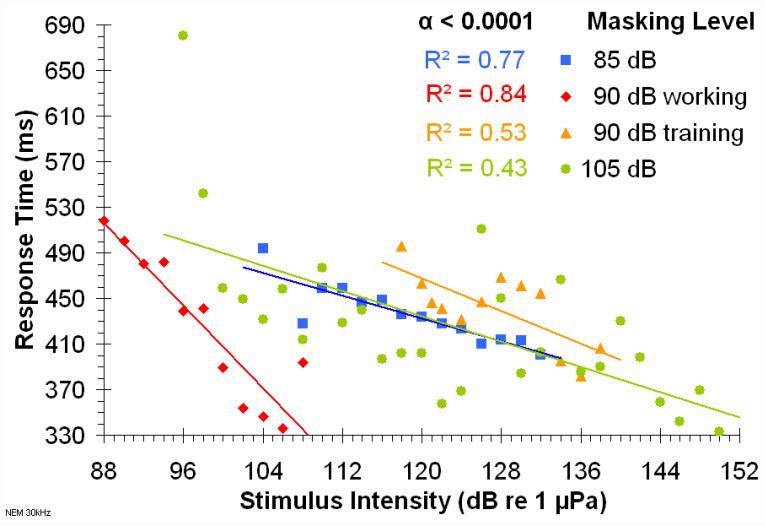

FIG. 40. Response time graph for NEM to 30 kHz stimuli.

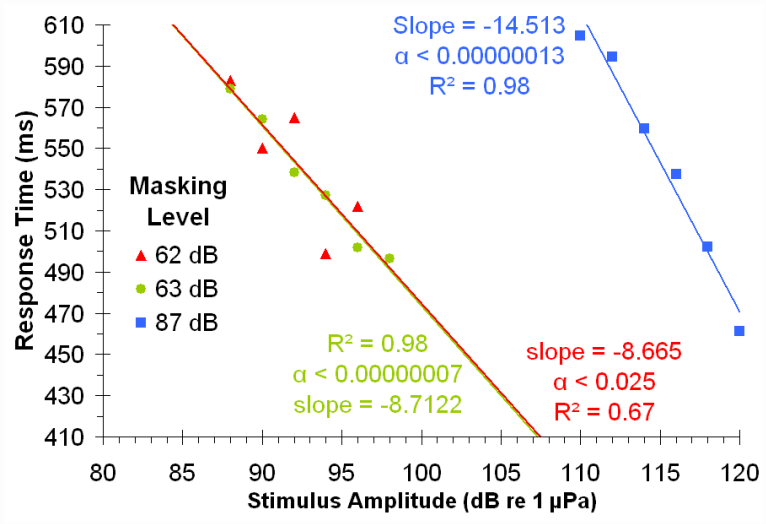

FIG. 41. Response time graph for MUK to 6 kHz stimuli.

relationship at 62 and 63 dB. At 87 dB, both the threshold and the response time relationship shifted to an increased stimulus amplitude with a steeper slope (Figure 41).

The threshold for MUK at 30 kHz at 75 dB and 85 dB masking were 107 and 117 dB respectively. The slopes of regression lines for response time to stimulus amplitude were approximately parallel (-6.76 and -6.40 ms/dB). MUK increased the response time by about 50 ms with an increase in masking noise level from 75 to 85 dB.

One of the whales, NOC, was only available for data collection in 1998 and 1999, so there is limited data for this subject. The four combinations of stimulus frequency and masking level with sufficient data for regression analysis are shown in Figure 42.

2. Within one masking level

In general, the relationship between response time and stimulus amplitude was similar across frequencies within one masking level.

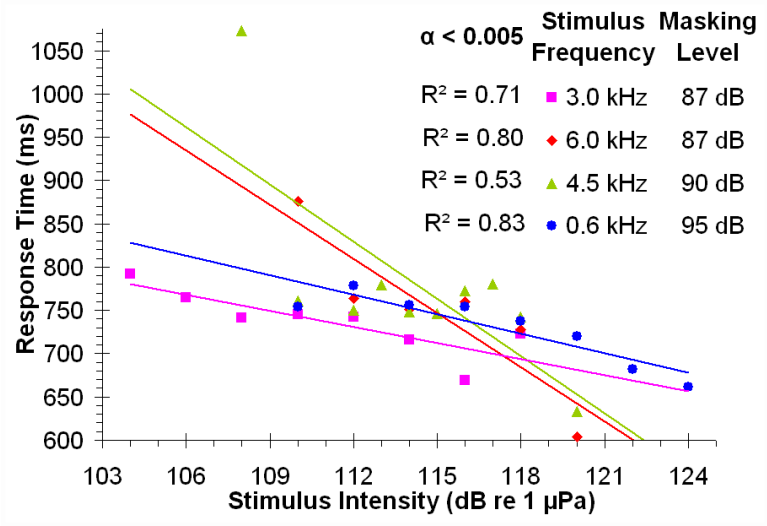

FIG. 42. Response time graph for NOC.

Data for NEM at 63, 87, and 90 dB masking noise levels showed the effects of frequency on the relationship between stimulus amplitude and response time within the same masking level.

NEM had similar response time to stimulus amplitude relationships at different frequencies. Response times were approximately the same within one masking level. NEM responded faster during working data collection to 30 kHz stimuli than at 4, 4.5, and 20 kHz stimuli. At 90 dB, the effect of a notch filter and the effect of training was apparent (see Figure 43). NEM responded to lower amplitude tones during working data collection than during training at about the same response time. NEM also responded to lower amplitude tones with a five kHz notch in the noise (centered at 20 kHz). The pattern of NEM responding to lower amplitudes with lower masking levels is consistent across 3, 4.5, and 6 kHz as seen in Figure 44. Note that within these frequencies, stimulus frequency had little effect on the relationship between stimulus amplitude and response time.

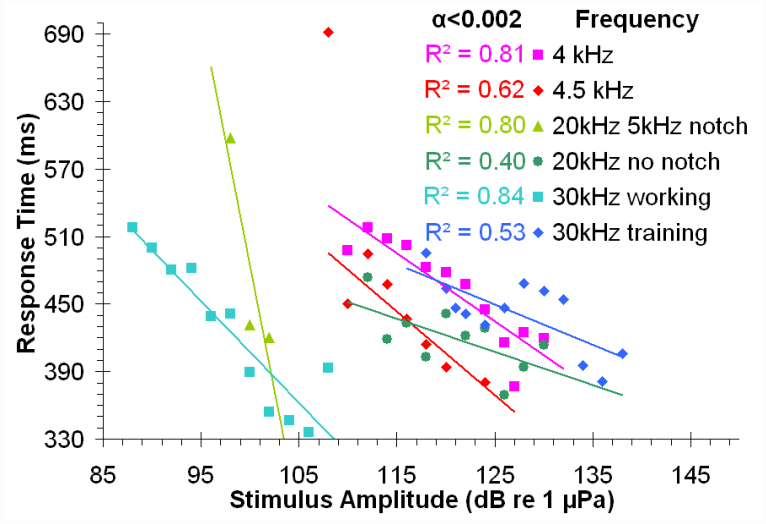

FIG. 43. Response time graph for NEM with 90 dB masking noise.

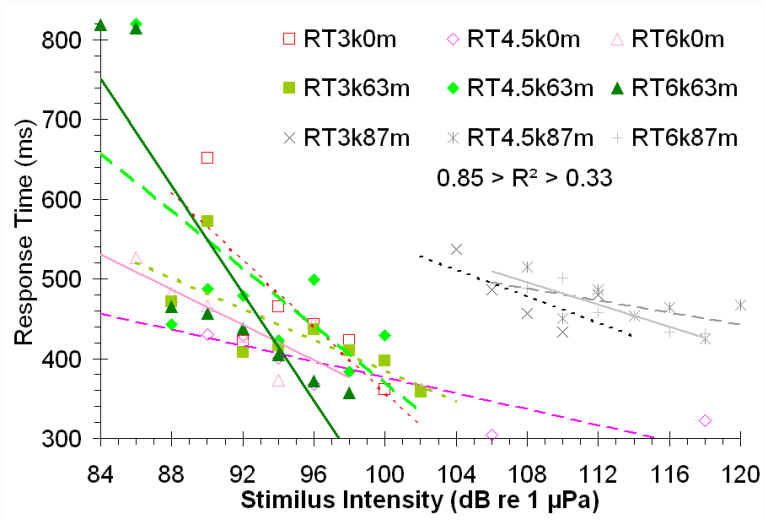

FIG. 44. Response time graph for NEM comparing response to 3, 4.5, and 6 kHz stimuli at 0, 63, and 87 dB re 1 μPa^2 Hz^{-1} masking noise.

There was no consistent pattern in the relationship between stimulus amplitude and response whistle amplitude or response whistle length.

D. Discussion

This study presents the first results comparing the simple response times of two cetacean species in hearing tests near threshold. Stimuli between 0.4 and 30 kHz were used, and masking noise levels between 0 and 95 dB re 1 μPa^2/Hz were applied.

1. Limitations in interpreting results

Results were presented on overall response times for six subjects. However, the specific analyses for regression of response times with changing amplitude could not be performed on two of these subjects. Too few trials had been performed with those subjects to permit performing regression analysis. The remaining four subjects had a sufficient number of trials to permit those analyses.

The design of this study was not based upon obtaining response times, but rather to determine hearing thresholds at a variety of frequencies. Because the hearing testing proceeded via the staircase method of estimating threshold, unequal numbers of stimuli at each amplitude were presented. This may violate some assumptions made for standard statistical analysis.

Regression analysis for simple response time is usually accomplished by taking the regression of the mean or median values of response times for each stimulus amplitude (Stebbins, 1966). In this study, some stimuli contributed more to the calculation of a regression analysis than others simply because of the difference in frequency with which certain stimulus amplitudes were presented. Overall, it seemed that at least 10 trials per stimulus amplitude are needed to give sufficient power for

statistical analysis. This is consistent with the procedures in studies of response times in terrestrial animals.

Due to the ambient bay noise, the application of masking noise was necessary to obtain a consistent hearing threshold. Response time studies are usually done in quiet conditions (Young, 1980). In both *Tursiops truncatus* and *Delphinapterus leucas*, a change in masking noise tended to shift the hearing threshold higher but not to change the response time near threshold.

2. Relevance to the broader theoretical questions

While intra-species variation was substantial, between-species comparisons showed a significant difference in response times. The white whales were significantly slower. Because white whales are significantly larger than bottlenose dolphins, the question of allometric change as a factor is immediately raised. In Figure 45, a power curve is fitted to points defined by the weights and mean response times for all subjects. The points for the four dolphins fall in the lower left part of the plot, while the two white whales fall on the right. The resulting exponent of the fitted power curve is 0.43. A typical allometric relation from physiological studies might have an exponent of about 0.67. The R^2 value of 0.74 indicates that increasing weight can explain almost three-quarters of the observed variation in response times.

The slower response times of white whales may be a constraint enforced by the physics of size and physiology. There is an interaction here between white whales as predators and their prey. Response times may play a role in choice of prey species, and thus have a shaping factor on the niche of white whales. Conversely, the faster response times of bottlenose dolphins may permit them to consistently succeed in taking prey items that would more frequently elude a white whale.

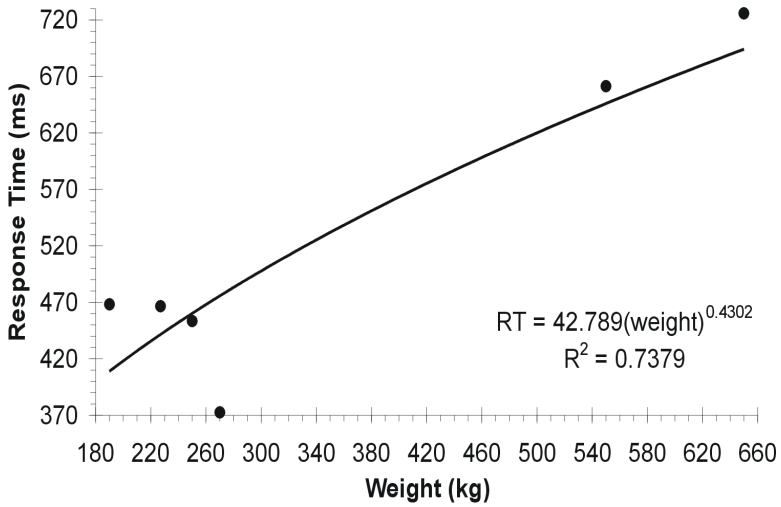

FIG. 45. Response times vs. weight for all subjects for stimuli near threshold.

E. Conclusion

For this study, white whales and bottlenose dolphins responded to higher amplitude stimuli faster than they responded to lower amplitude stimuli. This relationship between stimulus amplitude and response time is well known from previous work in terrestrial animals (Cattell, 1886b,c; Wells, 1913).

The average response time for bottlenose dolphins was 414 ms. The average response time for white whales was 672 ms. There was considerable variation between subjects within a species, but the difference between species was also found to be significant. White whales have longer response times, on average, than bottlenose dolphins. The difference in size may explain much of this difference in response times (see Figure 45).

CHAPTER IV

CONCLUSIONS

In this research, simple reaction times were found for two species of marine mammals, white whales and bottlenose dolphins, in both a listening task and a hearing threshold test. Response times were gathered using a method of free response and quantified from vocal responses. Comparisons between the two species were made. I will expand here upon some conceptual issues in response time studies and place the research findings in this framework.

A. A mental model of simple response time

As I previously discussed, a plot of response times versus stimulus amplitudes typically gives a curve with a linear portion with negative slope for stimuli well above threshold, and a portion with a steeper negative slope when stimuli are near threshold (see Figure 26). It is useful to think of these two regions of the plot in terms of two different linear relations (see Figure 46). One of these is the regime where hearing testing occurs, and is characterized by a steeper slope and higher miss rates in testing. The other is the regime where listening tasks occur, and it is characterized by a smaller negative slope and near-perfect hit rates for stimuli.

The hearing threshold test dealt with the question of "can the subject hear the signal?". The increase in response time as stimulus amplitude approaches threshold could be due to several factors. If the increase in response time is primarily sensory, the difference is in neurophysiological events during the sensory transduction of motion of the hair cells to electrochemical neural impulses or in the feature detection within the auditory cortex or both. If the increase in response time is primarily cognitive, then the difference is in processing and interaction of the thalamus, the

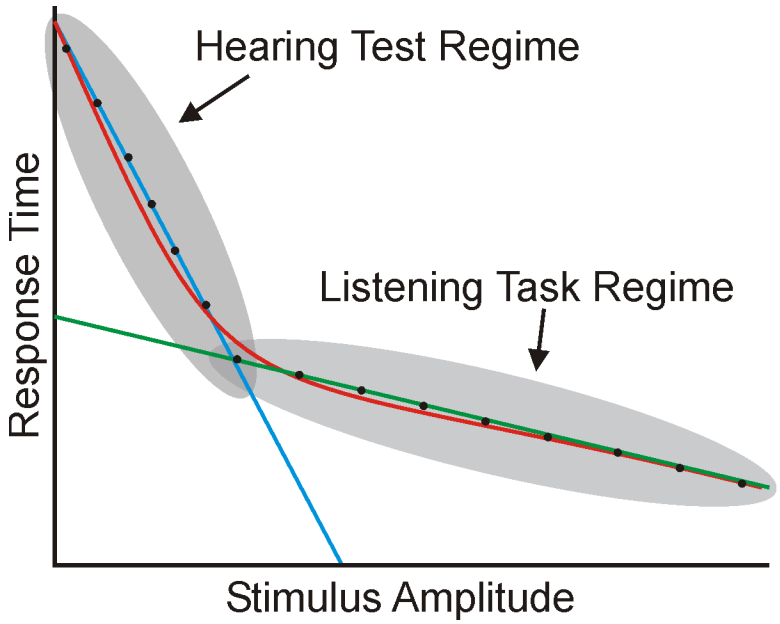

FIG. 46. Conceptual diagram of the relationships between simple response time, listening tasks, and hearing tests.

hippocampus, the amygdala, and other regions within the brain.

The listening task dealt with how fast the subject responded to a tone it could easily hear. The decrease in time as the stimulus increases in amplitude once the signal is easily detected, is probably due to cognitive processes.

These general principles can be applied to develop a set of expectations for simple response time work as it applies across species.

B. Expectations for inter-species comparisons and simple response time

Response time can be broadly divided into three parts: sensory, cognitive processing, and motor. In some studies of humans or rats, electromyography (EMG) or needle electrodes have been used to measure components of response time. Time to auditory evoked potentials is the sensory component. The time from activity of

the outgoing motor nerve or early EMG measure to the actual response is the motor component. The cognitive component is the time remaining when the sensory and motor components are subtracted from the total response time.

The sensory time includes the time from when the energy from the stimulus begins to excite reception at the sensory cells to preliminary processing in the appropriate sensory cortex. The sensory time is influenced by the structure of the sensory system, and for auditory stimuli sensory time should be similar across species with similar ears. Arthur Popper has said that the vertebrate ear across species is a set of variations upon a theme. The sensory time would be affected by differences in structure or in damage to the system, such as damage to the hair cells within the cochlea. The hearing threshold test primarily addresses factors in the sensory response time. Support for this comes from the findings with respect to increased response times for subjects in the listening task who had hearing deficits at higher frequencies. Their hearing deficits had to do with the sensory component, and these distinctly increased the response time.

The cognitive processing is done in parallel involving several parts of the brain. Differences in intelligence may effect the cognitive processing of the stimulus and choices of how to respond to that stimulus. This is the time component that probably varies the most both within and across species. Instructional and training methods also vary this component of response time. In some humans studies, the response time for the same task with different instructions were compared, and the response time differed depending upon the instructions given. Stebbins and Lanson (1961); Stebbins (1962); Stebbins and Lanson (1962) examined the effect of schedule and quantity of reinforcement and found these affected response time. Although Stebbins did not measure response time components, the variation was most likely in the cognitive processing component. Within a species, intelligence affects cognitive processing time,

but probably does not affect sensory or motor response time.

The motor processes start when the set of signals leave the brain on the motor nerves to coordinate the motor actions to produce the correct motor response. The different types of responses in different studies such as raising a hand, a vocal response, pushing a button with a foot, chin, or finger would affect motor response time. When motor response time within a species has been measured, it tends to vary less than the other two components of response time.

I will discuss this conceptual framework in relation to several aspects of the research reported in chapters II and III. Specifically, these are the performance of white whales and dolphins on the listening task and hearing test; a comparison of the performance of each species during the two studies; examination of the significance of these results with in the context of cross species comparison to terrestrial animals; a look at lessons learned; and the significance of this research.

C. Marine mammals and simple response time

1. Within-species relationships

a. Hearing test

The hypotheses examined included that increasing stimulus amplitude resulted in decreasing response time; that practice would reduce response time and variability; and that masking noise would shift hearing thresholds and response times.

In general, within one frequency and masking level, response times increased with decreasing stimulus tone amplitude, which was consistent with my hypothesis.

I expected the subjects' response times to become faster and less variable with practice based on the response time literature. Data from training sessions had slower response times than later working sessions (see Figure 40). A 5 kHz notch in masking

noise centered on the test frequency resulted in a lower threshold and shifted response times (see Figure 43). In some cases, there was a distinct change to a steeper slope at threshold (see Figure 39). There were few data points collected at the lower amplitudes and considerable variability when an animal did respond to these hard-to-perceive tones.

I expected masking noise to shift the thresholds to higher amplitude stimuli and, since response time reflects the threshold of detection, I expected that a higher amplitude stimulus tones would be needed to elicit the same response time. I thought that similar response times would be elicited by similar stimulus amplitudes when viewed relative to threshold.

Masking noise tended to shift threshold. There was considerable harbor noise so 0 dB masking really represents that there was no added white masking noise. Masking levels around 63 dB did not change threshold from the threshold when there was no masking noise. I speculated that 63 dB masking at the frequencies studied was not sufficient to mask ambient harbor noise. Since data was recorded based on threshold, stimuli of the same amplitude were often not included in both data sets if there was much difference in masking level. When the comparison was possible and the masking level differed by more than 2 dB, mean response time was faster at the lower masking level for stimulus tones of the same amplitude. To produce the same mean response time, stimuli were on the order of 20 dB higher amplitude in 8 7 dB masking noise than stimuli in 63 dB masking noise level (see Figure 41). This is a rough estimate only because there was considerable variation.

b. Listening task

Several hypotheses were examined with data from the listening task. I expected an inverse relationship between stimulus amplitude and response time. I expected

that response time might increase with both the shortest and the longest duration stimuli. I thought that response time across frequencies would reflect the shape of the audiogram. Based on human literature, I expected the young adult subjects to have the fastest response times. I expected response time to increase with increasing complexity of the listening task, as Hick (1953); Hyman (1953) had found in choice response time work.

In the listening task, I was primarily interested in the relationship between stimulus amplitude and response time. I expected to see increasing response times with decreasing stimulus amplitude. Multiple amplitudes were examined within most data sets. A data set only contained one duration of stimulus. I was able to determine that a similar relationship existed between response time and stimulus amplitude across a range of frequencies (Figure 18).

In general, response time was faster with increasing stimulus amplitude. In many, but not all, of the data sets linear regression had a good fit with r^2 values from 0.70 to 0.98 and showing an inverse relationship between response time and stimulus amplitude. This finding supports the finding that the subjects would respond faster to higher amplitude tones than to lower amplitude tones.

Effects of stimulus duration on response time are mixed in the literature (Wells, 1913; Raab and Fehrer, 1962). In some studies with very short stimuli, response time became slower as duration decreased.

In other studies with longer stimuli, response time became slower as duration increased. In short enough duration response times, lengthening duration reduces sensory response time as the stimulus becomes more detectable. Variation in longer stimuli affects cognitive processes as the brain processes how to respond when an easily detectable signal occurs. I thought perhaps that response time would increase as stimulus duration decreased below 8 ms. I expected that response time would

increase as response time increased above 100 ms.

One dolphin, MAU, did have slower response times to stimulus durations shorter than 4 ms. Another dolphin, MAY, responded slower to increasing stimulus duration beyond 175 ms. However, little can be stated about the effect of stimulus duration on response time. Several factors complicated finding a relationship of response time and stimulus duration in this study. Duration was not varied within one session. Factors such as variation in ambient sound within San Diego Harbor, variation in acoustic environment due to tide or wind, distractions due to other activity in the area such as divers or activity of other animals, and the internal state of the subject all could vary across sessions and influence response time. These non-stimulus factors could mask any relationship between response time and stimulus duration. The variable environment of San Diego Harbor emphasized the importance of varying the component of the stimulus to be related to response time, but even in a more consistent environment this component (in this case duration) should be varied within each session rather than across sessions.

Response time also decreased with increasing age. In human studies (Bellis, 1931), the fastest response times are from subjects in their teens and twenties. Based on this, I would have expected the fastest times from the youngest dolphins, APR and MAY. However, the oldest dolphins, TOD and MAU, were the fastest dolphins and also the most experienced dolphins, proficient in a wide variety of tasks.

I expected the response times across frequencies to reflect the shape of audiogram, with longer response times above 80 kHz and below 10 kHz. This reflection of the audiogram was demonstrated in the three dolphins with high frequency hearing deficits. An evaluation done in 1995 (Ridgway and Carder, 1997) indicated that MAU, MAY and SLA had some high frequency hearing loss. These subjects also had high miss rates and slow response times at the affected frequencies in the response time

listening task. The long latency to response where an animal has hearing loss fits this pattern. When the hearing loss is taken into account, this fits the hypothesis that I expected response time across frequencies to reflect the shape of the audiogram.

Based on the work of Hick (1953) and Hyman (1953) on choice response time and Shannon (1948) information theory, listening to multiple frequencies might result in longer response times relative to listening to one frequency. The listening dolphin receives the information (different frequency), although they respond to all frequencies in the same way. Data from three dolphins, MAU, MAY and SLA supported this hypothesis, while TOD's data was inconsistent with this hypothesis.

2. Comparison between white whales and bottlenose dolphins

When compared across species, some allometric relationships of metabolic measures have an exponent near 0.67 in a fitted power curve. On this basis, one might expect smaller species to respond faster than larger species. However, when two species were tested in the same experiment in terrestrial animals, humans and rhesus monkeys (Pfingst *et al.*, 1975a), the larger humans responded faster.

a. Hearing threshold test

The dolphins were significantly faster (414 ms) than the whales (672 ms) during the hearing test. In the hearing threshold test, the relationship between weight and response time for bottlenose dolphins and white whales yielded an exponent of 0.43 and an r^2 of 0.738. This indicates that almost three-fourths of the response time difference between species could be explained by weight.

b. Listening task

The whales were significantly slower (584.1 ms) than the dolphins (231.9 ms) in the listening task. The relationship between weight and response time for bottlenose dolphins and white whales yielded an exponent of 0.45 and an r^2 of 0.4893. This indicates that almost half of the response time difference could be explained by weight. The exponents (0.45 and 0.43) are similar for data sets both near and well above threshold.

c. Possible reasons for differences between response time in bottlenose dolphins and white whales

There are several reasons the bottlenose dolphins were faster than the whales. These include: length of neural pathways; intelligence or other aspects of cognition; differences in motor function; differences in training; differences in prey, social structure, or environment.

While the associated neural pathways are longer in the white whale, the transmission time is short enough that this difference in nerve length would not account for the difference in response time between the two species.

Within the cognitive portion of response time, intelligence is a possible factor affecting response times. Within humans, retarded subjects are slower to respond than are "normal" subjects. We do not have good measures of intelligence for comparison in cetaceans. Intelligence evaluations could be done that would compare problem solving, learning, awareness, and communication. Breeds of dogs have been compared by surveys of professional dog trainers. Perhaps marine mammal trainers could compare different species of cetaceans with which they have training experience. Several of the subjects in these studies, including both of the white whales, have

participated in numerous research projects and practical tasks. The same training methods have been used with both species with similar results, so this alone gives no indication that one of these species is more intelligent than the other.

The motor component of response time could also vary between species. When cetaceans whistle, they must pressurize the space below the phonic lips (Ridgway *et al.*, 1980; Amundin and Andersen, 1983; Ridgway and Carder, 1988; Cranford *et al.*, 2000; Elsberry, 2003). Perhaps it takes longer for white whales to prepare to whistle than for dolphins.

Since all subjects were trained by the same methods by the same trainers, I do not think differences in training can account for the difference in response time between the species.

Factors from the natural history of the subject species provide additional hypotheses to explain the difference in response times between white whales and bottlenose dolphins. Animals that eat fast moving active prey may need faster response times. White whales seem to eat more crustaceans and other benthic organisms (Freeman, 1968). Bottlenose dolphins often eat sound producing prey probably located through passive listening. There might be metabolic considerations related to white whales that live in the arctic and the more tropical bottlenose dolphins.

If component times were measured for bottlenose dolphins and white whales, then the information would help understand the difference in response time between the two species.

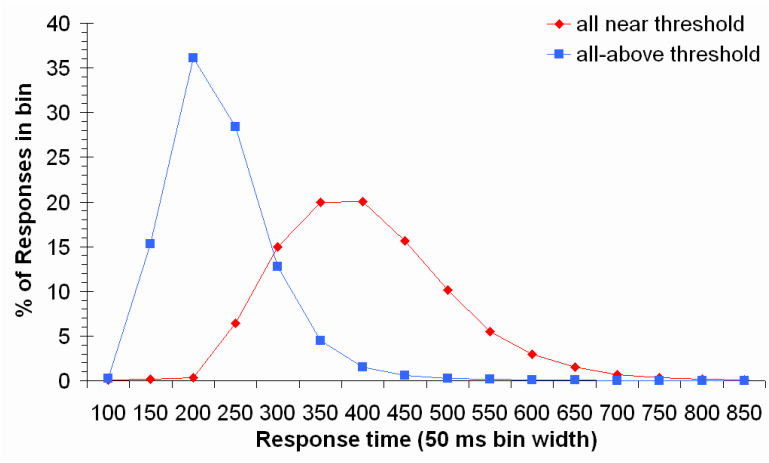

FIG. 47. Comparison of response times between stimuli well above threshold and stimuli near threshold for *Tursiops truncatus*.

3. Comparison between listening task and hearing test studies

a. Bottlenose dolphins

I expected that the dolphins would respond slower in the hearing threshold test than in the listening task. None of the dolphins participated in both studies. A comparison of the pooled dolphin response times is shown in Figure 47. The dolphins responded significantly faster to stimuli well above threshold (232 ms) than to stimuli near threshold (414 ms) as expected.

b. White whales

I expected that the whales would respond slower in the hearing threshold test than in the listening task. A comparison of response times for the whales is shown in Figure 48. NOC responded much faster for stimuli in the above-threshold listening task (379.6 ms) than for stimuli in the near-threshold hearing test (724.6 ms). MUK responded significantly faster for stimuli above-threshold (590.5 ms) than for stimuli

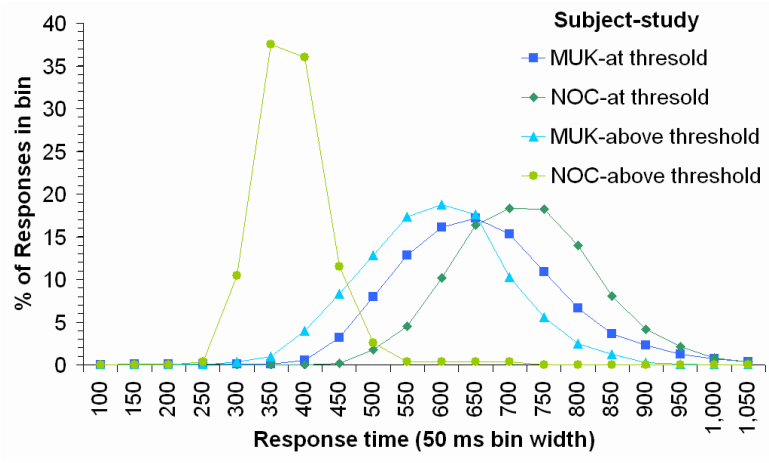

FIG. 48. Comparison of response times between stimuli well above threshold and stimuli near threshold for *Delphinapterus leucas*.

near-threshold (659.0 ms), but with less difference between the two studies than in NOC. Much of MUK's above-threshold data also did not follow the typical pattern of an inverse relationship between response time and stimulus amplitude. I speculate that MUK was not responding as quickly as she could in the above-threshold study. This is surprising, since she is usually a motivated subject who stays on task. Qualitative notes on environmental conditions and animal attitude were minimal on the listening task compared to the hearing threshold task. The more detailed notes during the hearing threshold study allowed data to be excluded due to environmental disturbances. This was not as much of an option with the less detailed notes taken during the listening task.

D. Comparison of marine mammals to terrestrial animals

It is difficult to compare response times across species in the literature due to differences in experimental methods and data reported. Figure 49 shows response times for

marine mammals, primates, rodents, and birds. Response times in marine mammals were similar to those for primates. There were considerable differences within one species across experiments. Variation in methods and stimuli probably account for much of this difference in response times.

For comparison purposes, I will examine the fastest and the slowest response times reported, both of which happen to be birds. Within these two species, differences in methods may account for the differences in response times. Starlings had the fastest response times (∼0.8 s). of the species studied, while house finches had the slowest response times (∼2 s). Differences in the species such as differences in social interactions, prey type, and breeding status might explain the difference in response times, but I suspect that most of the difference is due to differences in data collection methods.

Starlings had some of the fastest response times (∼80 ms). Pomeroy and Heppner (1977) were interested in how quickly a starling could respond to light or sound and how that might related to flocking movements. The starlings reacted with a startle response to onset of a 1 ms light or a 30 ms tone. The startle response was detected by a piezoelectric crystal on the perch. This required minimal movement of the animal and provided a natural, almost automatic, response.

House finches had some of the slowest responses (∼2000 ms). Dooling *et al.* (1978) were interested in audiograms and perception of loudness. The house finches were confined in a plastic tube and required to bite a switch to avoid an electric shock. The description did not say if care was taken that the subject was prepared to bite the switch before the onset of the tone. The stimulus for the house finch was a 5 s duration tone with a 50 ms rise time. This rise time is quite slow and the duration rather long. The subject had the full 5 s to respond to the tone in order to avoid the electrical shock. Long duration stimuli do not encourage quick response times.

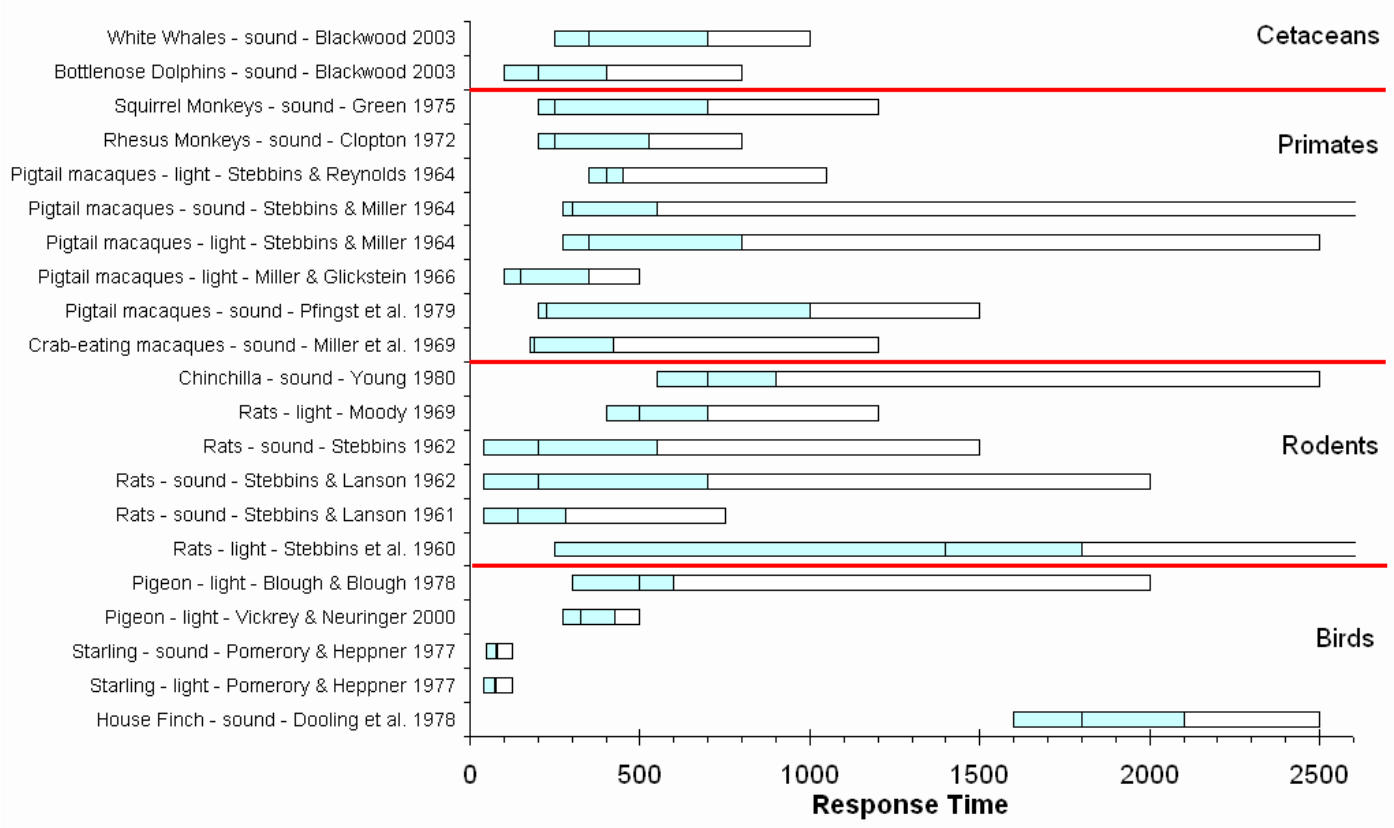

FIG. 49. Graph of response times in various species. The left end of the blue bar shows the estimated minimum response time. The left division within the blue bar shows the measure of central tendency for the response time well above threshold or for one of the fastest individuals. The division between the blue and white sections of the bar shows the measure of central tendency for the response time near threshold or for one of the slowest individuals. The white section shows the tail of the distribution of response times with the right end showing the estimated maximum response time.

As with the difference in response times between bottlenose dolphins and white whales, many factors could contribute to the difference in response times between the fastest species (starlings) and the slowest species (house finches). Some of these are similar such as differences in prey (sessile seeds or mollusks versus mobile insects and midwater fish), size, social structure differences, environmental effects, etc. Other factors include issues of seasonality. House finches eat seeds part of the year and collect insects to feed their offspring in the spring. Changes in brain mass have been noted in response to prolactin (visual) and testosterone (song) in the avian brain. The time of year or breeding status of the subjects may also effect response time in avian species.

The white whales and bottlenose dolphins were studied using a free-response method. Starlings were also tested in a free-response method, but their response was not trained, but rather was a natural startle response to a high-amplitude flash of light or tone burst. Most other non-humans species were studied using discrete trials. The studies with the least variability used a method with careful control of environment, subject mental and physical status, and carefully designed discrete trials (Stebbins and Lanson, 1962).

These studies on cetaceans were the only studies to compare two species where the same training and data collection methods were used. The only other study to include two species included humans and rhesus monkeys, however, the humans received verbal instructions while the rhesus monkeys were trained via operant conditioning. The humans responded faster although humans are also much larger (Pfingst *et al.*, 1975a).

Since response time has also been related to intelligence, perhaps that was the major factor in the human/monkey comparison. The humans were also verbally instructed to respond as fast as possible, while operant conditioning was used to

train the monkeys on the response time task. This difference in instruction/training may also contribute to differences in response times between monkeys and humans even though the data collection methods were the same.

E. Lessons learned

Experience gained during this work generated suggestions for future work. If we are to systematically examine inter-species differences in the future, we need to be careful about how experiments are conducted so they will be comparable. Marine mammals challenge researchers to develop new protocols when standard procedures used for many small-bodied terrestrial species are not applicable.

When studying sound, it is desirable to eliminate extraneous acoustical energy (noise). The ideal acoustical environment would feature free-field propagation of the signal of interest, no reflection or reverberation of the signal from boundary surfaces, and no non-signal acoustic energy present in the environment. In acoustical laboratories, this state is approached by the use of anechoic chambers. Unfortunately, attaining these ideal conditions is not practical for work with marine mammals.

For marine mammal work, there are essentially three acoustic environments available for the researcher. The first and most well-known is some sort of tank. Tanks suffer from high reflection and reverberation levels and also may have significant machine noise associated with pump and filtration systems. Significant effort must be expended to reduce the noise levels in tanks, such as by lining a tank with a layer of well-soaked redwood planking. The second environment is in a near-shore environment. In this case, there may be less reflection and reverberation than would be the case for a tank, but other noise sources may be present. These extraneous noise sources include those from wind, wave, seismic, biological, and anthropogenic

sources. An important noise source in tropical and semi-tropical regions is that of snapping shrimp, which produce high-amplitude broadband noise pulses. Due to their numbers, this noise may be the predominant non-signal component of a near-shore environment. The third environment is the open ocean. Wind and wave noise may still apply, but many of the other extraneous noise sources are either absent or much reduced in amplitude. A drawback to open ocean work with marine mammals is that the animals must be trained to reliably work and return. Working in the open ocean also typically requires one or more ships, which increases the cost of research considerably. For all marine mammal work environments, a very efficient acoustic reflector exists in the form of the air-water interface of the water's surface. The choice of working environment for acoustical studies has to trade-off availability and cost-effectiveness for the desired noise and acoustic properties.

To really examine the relationship between a stimulus parameter (duration for example), that parameter should be varied within each data collection session while other factors are held constant. In these studies, I was primarily interested in the relationship between response time and stimulus amplitude. Test tone amplitude varied within each dive in most data sets in both studies. However, since duration did not vary within any one session, other factors could confound examination of the relationship between response time and duration. The variability in environmental noise made this particularly apparent in this study, but this would be an issue even in a more controlled environment.

Each subject should experience the same test conditions and be given the same number of trials in each testing condition. Due to the variability of response times, even in controlled conditions, between 20 and 50 responses per test condition should be given to obtain a good measure of central tendency. When possible, the range of amplitudes of stimuli should go from near threshold to well above threshold during the data collection session.

A series of questions for the trainers would assist in plotting variations in performance as they relate to mood or other factors in the subjects daily routine.

F. Significance of the research

1. Inter-species comparison

This study is the first to compare simple response times of two species of marine mammals. Between-species comparisons are rare in the response time literature. This is the first study where two species were studied with the same training and data collection methods applied to both species. There was a study (Pfingst *et al.*, 1975a) where the same data collection methods were used for humans and rhesus monkeys. However, the humans were instructed in English and the monkeys were trained using operant conditioning. To make a comparison between humans and non-humans, the humans would need to be trained non-verbally. Subjects could be told they were playing a training game, and could be shaped using operant conditioning just as the non-human subjects are prepared for research projects. The process of shaping subjects without verbal instruction might crossover well for young children, or those with brain damage.

Since this is the first study to look at more than one species using the same training and data collection methods, it allows a first look at the relationship between

body size and response time. The relative size of the animals appears to explain much of the difference found in response times between bottlenose dolphins and white whales. However, there are only two species compared. To test this intriguing trend other species need to be tested. Orcas and harbor porpoises have also successfully participated in hearing tests and would extend the size range. To test the size factor, other species similar in size to bottlenose dolphins (*Tursiops truncatus*), such as spotted dolphins (*Stenella* spp.) need to be tested to see if they have similar response times.

This is the first study that compares auditory response times at the same frequency and different masking levels in marine mammals and perhaps even in any non-human species. Masking noise from human sources (shipping, drilling, acoustic ocean thermography) and natural sources (ice floes, seismic activity, wave and wind noise) occur in the oceans and affect animals' ability to hear and their responses to what they can hear. This looks at response times as they are effected by factors in a more biologically meaningful environment.

2. Comparisons to terrestrial species

Some hypotheses from the human literature were supported, such as the inverse relationship between response times and stimulus amplitude. Other hypotheses, such as the relationship between age and response times in adults, were not supported.

3. Information theory and simple response time

I examined the possibility that multiple stimulus types within a simple response time task also increased response time, just as increasing the numbers of choice responses increase response time. Three subjects, MAU, MAY, and SLA, were faster at responding to data sets consisting of only one frequency than in responding to data

sets with multiple frequencies. Transfer of Shannon information requires perception, but not action, by the recipient. Human subjects might have been instructed to think of all tones as the same independently of the frequency, or they might have been instructed to think of the different frequencies as different categories of stimulus, even if there was only one type of response. With the dolphins, we do not know how they internalized the different frequency tones.

Since I only compared single frequencies to multiple frequencies (5 for APR and 8 for MAU, MAY, SLA and TOD) there was no way to try to fit the data to Hick's law:

$$RT(seconds) = k * log_{10}(n + 1) \tag{4.1}$$

where n is the number of stimulus types.

The results were intriguing enough that the studies should be extended to test Hick's law. This could be done by checking the fit of multiple stimulus types (in this case, frequency) to Hick's Law even within a simple response time task, multiple frequency data sets of 2, 4, and 6 frequencies would be needed in addition to the sets with 1 and 8 frequencies.

4. Automated method for quantifying response times for vocal responses

My automated response detection algorithm provided a standardized procedure available to collect response time data for subject species unsuited to button pressing or key pecking. An automated response detection algorithm was developed for data collection with acoustic stimuli near threshold. The high accuracy (98%+ overall correct classification of responses) of this algorithm was achieved using parameter sets tuned for the ensemble of responses from individual subjects. The design and

implementation process used in construction of this algorithm may be usefully applied in other behavioral research projects. Deployment of this method would put vocal responses on a similar automatically quantifiable basis as button presses and other motor responses, which usefully extends the range of behaviors which may be considered in future response time work.

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